Rangelands in a Changing Climate: Impacts, Adaptations, and Mitigation

BARBARA ALLEN-DIAZ, USA

Principal Lead Authors:

F.S. Chapin, USA; S. Diaz, Argentina; M. Howden, Australia; J. Puigdefábregas, Spain; M. Stafford Smith, Australia

Lead Authors:

T. Benning, USA; F. Bryant, USA; B. Campbell, New Zealand; J. duToit, Zimbabwe; K. Galvin, USA; E. Holland, USA; L. Joyce, USA; A.K. Knapp, USA; P. Matson, USA; R. Miller, USA; D. Ojima, USA; W. Polley, USA; T. Seastedt, USA; A. Suarez, Cuba; T. Svejcar, USA; C. Wessman, USA

Contributing Authors:

W.N. Ekaya, Kenya; J. Ellis, USA; L.D. Incoll, UK; J. Kinyamario, Kenya; C. Magadza, Zimbabwe; T. Oikawa, Japan; O. Sala, Argentina; C. Scoppa, Argentina; N. Maceira, Argentina; R. Rodriguez, Argentina

CONTENTS

Exec	utive Summary	133	2.6.	Boundary Changes	141
2.1.	Introduction: Description of the World's		2.7.	Regional Variation	142
	Rangeland Resources	134		2.7.1. Low-Latitude Regions	142
				2.7.2. Middle-Latitude Regions	143
2.2.	Climate Variables	135		2.7.3. High-Latitude Regions	145
	2.2.1. Precipitation and Temperature	135			
	2.2.2. Effects of Altered Atmospheric CO ₂		2.8.	Modeling Rangeland Ecosystem Response	146
	Concentrations on Rangelands	136			
	2.2.3. Other Important Trace Gases	138	2.9.	Human Adaptation	147
2.3.	Ecosystem Variables	138	2.10.	Mitigation	148
	2.3.1. Herbivory	138			
	2.3.2. Fire	139	2.11.	Research Needs	151
	2.3.3. Land Use and Management	139			
			Refer	rences	152
2.4.	Issues of Scale	140			
2.5.	Extreme Events	141			

EXECUTIVE SUMMARY

Rangelands (i.e., grasslands, shrublands, savannas, hot and cold deserts, and tundra) occupy 51% of the terrestrial land surface, contain about 36% of the world's total carbon in above and belowground biomass (Solomon *et al.*, 1993), include a large number of economically important species and ecotypes, and sustain millions of people. Rangelands support approximately 50% of the world's livestock and provide forage for both domestic and wildlife populations (Briske and Heitschmidt, 1991).

Doubled-CO₂ climate-change scenarios provided for IPCC Working Group II (Greco *et al.*, 1994) were used to analyze the regional impacts of altered climate regimes on rangeland resources. Results indicate:

- Rangeland vegetation is found where mean precipitation, temperature, elevation, and latitude interact to provide sites suitable for herbaceous species, shrubs, and/or open stands of trees. However, carbon cycling, productivity, and species composition in any region is directly related to the highly variable amounts and seasonal distribution of precipitation and is only secondarily controlled by other climate variables. Small changes in the frequency of extreme events may have disproportionate effects on what managers must cope with in rangeland systems (High Confidence).
- CO₂ increases are likely to result in reductions of forage quality and palatability because of increasing carbon to nitrogen ratios. These effects will be more common in lower-latitude rangelands where low nutritional value is already a chronic problem (Medium Confidence).

- Boundaries between rangelands and other biomes are likely to change with changes of climate: directly, through climate-driven changes in species composition, and indirectly, through changes in wildfire regimes, opportunistic cultivation, or agricultural release of the less-arid margins of the rangeland territory. These effects will be more common in the temperate rangelands (High Confidence).
- Climatic warming may cause tundra to become a net source of carbon dioxide. Temperature increases in the tundra will reduce species richness, especially of insect-pollinated forbs (Medium Confidence).
- The extensive use of rangelands suggests that strategies to reduce greenhouse gas emissions must focus
 on maintaining or increasing carbon sequestration
 through better soil and vegetation management and
 reducing methane by altering animal production systems (High Confidence).
- Human adaptive strategies for coping with climatechange effects on rangelands include the preservation of an extensive spatial scale in management units and the development of viable marketing systems capable of absorbing opportunistic variations in number and/or kind and class of animals (Medium Confidence).

2.1. Introduction: Description of the World's Rangeland Resources

Rangelands occupy approximately 51% of the terrestrial surface of the Earth, or 68.5 million km² (Lean *et al.*, 1990; Prentice *et al.*, 1992). Rangelands include unimproved grasslands, shrublands, savannas, and hot and cold deserts. For the purposes of this assessment, tundra and improved pastures are included here, while hot deserts are described in Chapter 3.

The primary use of rangelands has been and is for grazing by domestic livestock and wildlife. Rangelands support fifty percent of the world's livestock (WRI, 1992) and provide forage for both domestic and wild animal consumption (Briske and Heitschmidt, 1991). Rangeland management systems vary from nomadic pastoralism to subsistence farming to commercial ranching. Markets are largely externally driven, with extensive social systems in contrast to commercial agriculture. Overgrazing (the result of animal consumption exceeding carry capacity) has been and is common to rangelands throughout the world (WRI, 1992).

Most of the forage consumed by domestic livestock (cattle, sheep, goats, buffalo, and camels) is supplied by rangelands in Africa and Asia (Table 2-1). Other regions of the world support many fewer animals from rangeland forage resources. Numbers and kinds of domestic and wild grazing animals vary by region.

The distribution of the world's rangelands falls on continua from wet to dry, fertile to infertile, and hot to cold (Figure 2-1). Holdridge (1947) arrayed the world's vegetation into life zones based on mean annual growing season temperature (°C), average annual precipitation, an index of precipitation divided by potential evapotranspiration (PET), and latitude (Figure 2-2). Rangelands occupy areas where combinations of temperature, precipitation, PET, and latitude prevent occupation by dense stands of trees. Figure 2.2 is a good display of the types of ecosystems covered in this chapter, although the hot deserts

are described in more detail in Chapter 3. Holdridge and others (Walter, 1973; Bailey, 1989; Prentice *et al.*, 1992) recognized that seasonality of precipitation, soil factors, herbivory, and fire are additional important factors in determining local vegetation composition and structure. Interactions between plant-available moisture and available nutrients also are crucial to rangeland structure and composition (Walker, 1993).

Rangeland ecosystems are diverse (Table 2-2), and stores of carbon both above and below ground vary by ecosystem type (Solomon *et al.*, 1993). Carbon (C) stored in the world's rangeland vegetation has been estimated by the BIOME 1.1 model at 749.7 Gt (Solomon *et al.*, 1993), although annual net primary productivity varies widely (Barbour *et al.*, 1987). Carbon in the world's rangeland soils has been estimated at 591.6 Gt, or 44% of the world's total soil carbon (Solomon *et al.*, 1993). Preindustrial levels of soil C (to 20 cm depth) in grasslands alone have been estimated at approximately 96 Gt (Ojima *et al.*, 1993b). Current soil C stocks for these grasslands (based on Ojima *et al.*, 1993b) are estimated at 81–164 Gt, based on land-cover estimates of Bailey (1989) minus estimated land under cultivation in these regions provided by Prentice *et al.* (1992).

In rangelands, the amount and timing of precipitation are the major determinants of community structure and function. Other driving forces that determine plant community composition, distribution, and productivity include temperature, fire, soil type, and herbivory. These driving forces prevent species senescence and allow for periodic rejuvenation by eliminating aboveground biomass and organic debris and thereby liberating nutrients. Most rangelands do not exist in a state of equilibrium, nor do they exhibit linear successional trends; rather, they fluctuate from one state to another depending on rain, fire, grazing, and other anthropogenic factors (Westoby et al., 1989; Stafford Smith and Pickup, 1993; Hobbs et al., 1991; Stafford Smith, 1994). Most rangelands are nonequilibrial within the range of climatic conditions that they currently experience. Underlying trends in climate change may cause some compositional states to become more likely (e.g., the

Table 2-1: World livestock and their dependence on rangeland resources. Percent of feed from rangeland is an estimate based on figures for the amount of grain fed to livestock; the assumption is that the rest of the feed source supporting the animals is from rangeland [World Resources, 1992–1993 (UNEP/UNDP)].

	Land Resources	(1,000 hectares)	Animal Units (1,000 animals)					
-	Permanent	Woodland	a .	Sheep,	Buffalo,	Feed from		
Region	Pasture	or Other	Cattle	Goats	Camel	Rangeland		
Africa	890,889	1,200,565	183,715	372,038	16,877	82%		
North, Central America	368,631	779,838	161,050	33,566	9	35%		
South America	447,863	237,792	262,254	134,759	1,190	54%		
Asia	694,251	1,043,666	389,730	640,938	138,814	84%		
Europe	83,177	92,524	124,900	166,023	370	45%		
Former Soviet Union	371,500	678,829	118,767	145,588	707	45%		
Oceania	436,622	199,523	30,862	223,838	ND	50%		

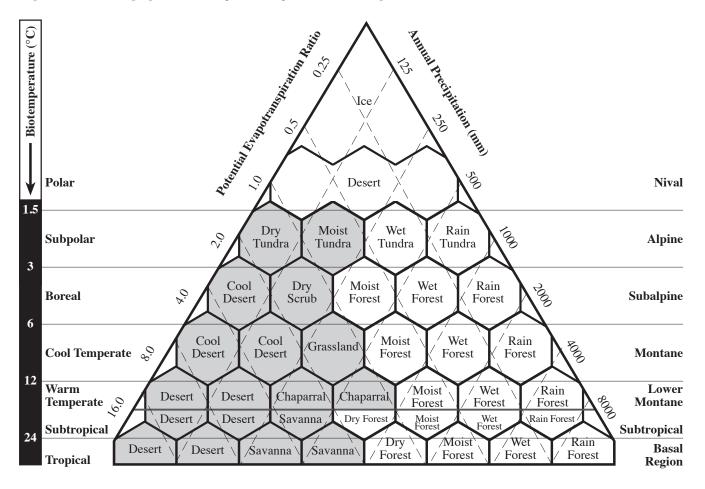


Figure 2-1. Distribution of rangeland types using the Holdridge classification system (Holdridge, 1947) as modified by Cramer and Leemans (1993). Biotemperature is the mean value of all daily mean temperatures above 0°C, divided by 365. The heavy line between Warm Temperate and Subtropical zones represents the boundary for risk of a killing frost. The demand of plants for moisture is represented by mean annual precipitation and potential evapotranspiration ratio. The shaded areas are rangeland types discussed in this chapter.

shrub invasion process is hypothesized to be linked to climate shifts or to grazing in the United States). However, in managed rangeland systems, management is as likely, at present, to maintain the systems in the desired state. In many areas, however, poor management of rangelands enhances the changes likely to be caused by climatic/atmospheric change—for example, by increasing the ratio of woody to herbaceous vegetation.

2.2. Climate Variables

2.2.1. Precipitation and Temperature

Among climatic variables, those related to water availability and water balance appear most influential in controlling the geographic distributions of rangeland vegetation (Stephenson, 1990) and production (Rosenzweig, 1968; Webb *et al.*, 1983; Sala *et al.*, 1988). There is a strong linear relationship between aboveground net primary productivity (ANPP) and annual precipitation in rangeland ecosystems (Rutherford, 1980; Webb *et al.*, 1983; Le Houerou, 1984; Sala *et al.*, 1988; Scholes, 1993), with typically 90% of the variance in primary production accounted for by

annual precipitation (Le Houerou and Hoste, 1977; Webb *et al.*, 1978; Walter, 1979; Foran *et al.*, 1982; Sala *et al.*, 1988).

Temperature does not account for a significant fraction of the ANPP variability among years in a particular region (Sala *et al.*, 1988; Lauenroth and Sala, 1992; Sala *et al.*, 1992). However, temperature appears to be the major climatic variable controlling the process of decomposition in grasslands and other rangeland types (Jenkinson, 1977; Meentemeyer, 1984; Burke *et al.*, 1989). It has been shown experimentally that decomposition rates increase rapidly with temperature, provided that there is enough water (Meentemeyer, 1978, 1984; Schimel, 1988; Holland *et al.*, 1992; Ojima *et al.*, 1993a; Parton *et al.*, 1993; Townsend *et al.*, 1992; Burke *et al.*, 1995a).

Temperature also affects C_3/C_4 species composition of grasslands (Sims, 1988) because of differences in optimal growing conditions (see Chapter A). The distribution (Terri and Stowe, 1976; Tieszen *et al.*, 1979) and seasonal activities of C_3 and C_4 grasses (Kemp and Williams, 1980; Hicks *et al.*, 1990) often are highly correlated with temperature. This is not necessarily true for dicotolydenous plants such as legumes, however (Ehleringer and Field, 1993).

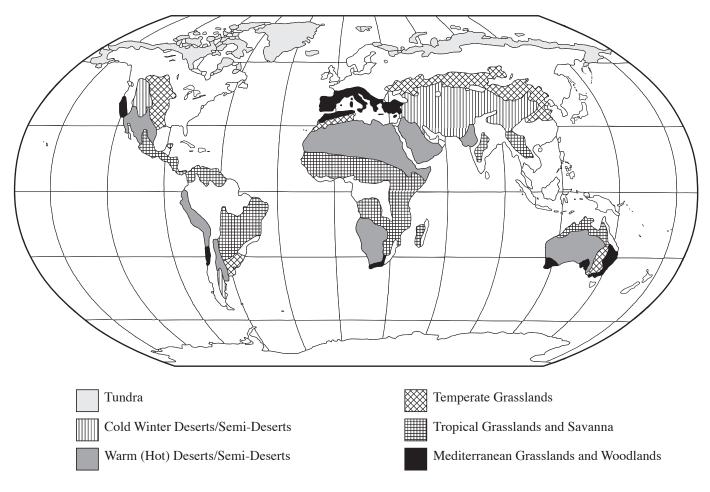


Figure 2-2: Geographic distribution of the world's rangelands (Lean et al., 1990; Bailey, 1989; Prentice et al., 1992).

2.2.2. Effects of Altered Atmospheric CO₂ Concentrations on Rangelands

Most research on rangeland plant response to elevated CO₂ has focused on responses of individual plants (Bazzaz and McConnaughay, 1992; Idso and Idso, 1994). A wide range of plant parameters have been measured (see Chapter A), and as a rule, studies show that increasing CO₂ levels increase photosynthesis, water-use efficiency (WUE), above- and belowground productivity, and nitrogen-use efficiency (NUE) and decrease stomatal conductance, transpiration, and whole-plant respiration (Wong et al., 1979; Kimball, 1983; Webb et al., 1983; Strain and Cure, 1985; Morison, 1987; Smith et al., 1987; Idso, 1989; Bazzaz, 1990; Kimball et al., 1990; Bazzaz and McConnaughay, 1992; Kimball et al., 1993; Rozema et al., 1993; Zak et al., 1993; Gifford, 1994; Idso and Idso, 1994; Rogers et al., 1994). For example, controlledenvironment studies have repeatedly demonstrated that growth and net photosynthesis of C₃ plants, including woody species such as Prosopsis glandulosa (Polley et al., 1994), are highly responsive to CO₂ when it is increased over concentrations representative of the recent and prehistoric past (Gifford, 1977; Baker et al., 1990; Allen et al., 1991; Polley et al., 1993a).

Responses to CO₂ increase are not necessarily consistent across species or under all environmental conditions. Two

processes—increased photosynthesis and reduced transpiration—typically contribute to the positive influence of CO₂ on plant WUE. Atmospheric CO₂ directly affects the coupling between climatic water balance and vegetation by altering the efficiency with which plants use water. The effect of CO₂ on water use may be more important in water-limited rangelands than in moist grassland systems or irrigated agricultural land. Elevated CO₂ can result in a slower depletion of soil water in drought-stricken rangeland grasses where there is no change in leaf area due to limitations such as nitrogen availability (Owensby *et al.*, 1993; Campbell *et al.*, 1995a).

Plant responses under variable environmental conditions or in competitive settings do not necessarily match responses under steady-state conditions and/or in the absence of competition. That is, results from studies in pots cannot automatically be assumed relevant to plants in native ecosystems (Nie et al., 1992; Campbell and Grime, 1993; Owensby et al., 1993; Campbell et al., 1995b). Competitive outcome in response to elevated CO₂ can be difficult to predict because of the feedback between litter quality, soil, and plant production (Schimel et al., 1991; Bazzaz and McConnaughay, 1992; Ojima et al., 1993b; Newton et al., 1995). In natural ecosystems, nutrient limitation may influence the response of individual species (Billings et al., 1984; Wedin and Tilman, 1990;

Table 2-2: Major rangeland vegetation types.

Туре	Area (10 ⁶ km ²)	Major Characteristics	General Climate	Current C Above Ground	Stores (Gt) Below Ground
Cool Semi-Desert	4.91	Sparse shrubs dominate	Cold winters with snow, hard frosts; 50–250 mm annual precipitation; meets <28% of demand	3.0	30.7
Cool Grass Shrub	7.17	C ₃ grasses dominate, with or without shrubs	Strong summer/winter peaks in precipitation; averages 400–1600 mm; meets 28–65% of demand	5.8	70.9
Warm Grass Shrub	9.84	C ₄ grasses dominate	Strong seasonality in precipitation; dry season of ~5 months; rainfall meets 18–28% of demand	13.0	87.2
Hot Desert	20.70	Shrubs less than 100% cover	Mild winters; 50–250 mm precipitation; rainfall meets <18% of demand	6.3	63.1
Tropical Savanna/ Dry Woodland	17.18	C ₄ grasses/sedges dominate, with significant discontinuous cover of trees and shrubs	Strong seasonality in precipitation; rainfall meets 45–80% of demand	78.6	124.8
Xerophytic Woods/ Shrubland	10.63	Widely variable woodlands, sclerophyllous shrubs, and annual grasses	Prolonged summer drought of 2–11 months; rainfall meets 28–45% of demand	45.5 s	80.9
Tundra	11.61	Dominated by herbaceous species	Temperatures generally <10°C; variable precipitation	5.9	134.0

Conroy, 1992; Comins and McMurtrie, 1993), and complex feedbacks between plant and soil microorganisms may arise (Diaz et al., 1993). In some studies, soil microbial respiration rate is greatly enhanced under lower CO₂ conditions and reduced under higher CO₂ conditions in the laboratory (Koizumi et al., 1991) and in the field (Nakadai et al., 1993). Experimental doubling of CO₂ concentration has relatively little effect on plant growth in Arctic tundra, presumably because of constraints of low nutrient supply (Tissue and Oechel, 1987; Grulke et al., 1990). Increased levels of carbon dioxide may increase individual plant production, but the effect on whole-ecosystem production is less clear, as resource augmentation has been shown to decrease species diversity and differentially affect individual species growth (favoring pioneer species) (Wedin and Tilman, 1990; Bazzaz, 1993).

Plants grown in CO₂-enriched environments tend to have reduced mineral concentrations (except phosphorus) relative to those grown at ambient CO₂ levels (Conroy, 1992; Overdieck, 1993; Owensby *et al.*, 1993). Decreases in nitrogen (N) concentration with elevated CO₂ have been demonstrated with a wide array of species (Conroy, 1992; Coleman *et al.*, 1993; Diaz *et al.*, 1993; Overdieck, 1993). These changes in mineral concentration in plants make them less palatable to herbivores and may even influence herbivore health and production (Fajer *et al.*, 1991). Increased concentrations of carbon-based, nonpalatable secondary compounds

could also deter herbivory, although the evidence for this process is weaker (Ayres, 1993; Diaz, 1995). The influence of elevated CO₂ on nutrient cycling must also be considered in light of potential impacts on litter inputs and litter quality. Reduced nitrogen concentrations may reduce the rate of decomposition, thereby slowing nutrient cycling and energy flow (Bazzaz and Fajer, 1992; Schimel *et al.*, 1994). In addition, surplus C may be converted to secondary compounds such as tannins, which decompose slowly.

According to controlled-environment studies, C_3 plants tend to be more responsive to CO_2 than are C_4 ones (see Chapter A). This effect is not always sustained at the community level, however. For example, Owensby *et al.* (1993) report that production of a C_4 -dominated tallgrass prairie increased when exposed to elevated CO_2 , apparently as a result of higher water-use efficiency, but other studies have detected no effect on production, flowering, or growth rates (Polley *et al.*, 1994; Korner and Miglietta, 1994). Data from grasslands ungrazed for 100 years in Rothamsted, UK, suggest that rising CO_2 does not affect herbage yield (Jenkinson *et al.*, 1994).

Differential species responses to CO_2 could also have implications for species assemblages and plant-community dynamics. Therefore, the outcome of multispecies experiments is not readily predictable from the behavior of individual species (Bazzaz, 1992, 1993; Korner, 1993; Diaz, 1995).

2.2.3. Other Important Trace Gases

The atmospheric concentrations of a number of important trace gases apart from CO_2 have increased (Cicerone and Oremland, 1988; IPCC, 1990, 1992), but their effects on rangeland ecosystems are not clear because they do not directly affect the rates of ecosystem processes or community dynamics (Mooney *et al.*, 1987).

A number of factors influence CH₄, NO, and N₂O emissions from rangeland ecosystems: deposition of nitrogen, nitrogen fertilization, changing climate, elevated CO2, ozone influences on plant production, changing plant community composition, changing animal populations, and changing land use (Schimel et al., 1990, 1991; Ojima et al., 1993a; Parton et al., 1994). Many of these factors are likely to respond non-linearly to climate changes. Changing precipitation and temperature directly affect the production of both NO and N₂O by regulating microbial activity (Firestone and Davidson, 1989). With abundant substrate, increasing temperatures generally increase rates of production, but changing soil moisture could decrease the rates of production. With no change in diet, more animals would result in greater N₂O production (Bouwman et al., 1995). However, all of the other factors listed are likely to change emissions through regulation of the nitrogen cycle. The greatest increase in emissions will occur when nitrogen supply exceeds plant demand, because this directly increases the nitrogenous substrates available for volatilization and leaching.

Many of the factors that influence nitrogen gas emissions also influence net methane emissions, but the influences are not necessarily in the same direction. Conversion of forests to pastures, fertilization, and, probably, nitrogen deposition decrease soil methane consumption (Mosier *et al.*, 1991; Keller *et al.*, 1993; Ojima *et al.*, 1993a). Any factor that enhances primary productivity, such as elevated CO₂, N deposition, or fertilization, is likely to increase methane emissions because methane production is limited by substrate availability (Whiting and Chanton, 1993; Dacey *et al.*, 1994; Valentine *et al.*, 1994; King and Schnell, 1994; Hutsch *et al.*, 1995). The possible extent of this enhancement is not yet clear. On the other hand, factors that decrease primary production (and thus CO₂ uptake) or pH, like ozone and acid rain, could have the opposite effect (Yavitt *et al.*, 1993).

Increases in animal populations capable of emitting CH_4 via enteric fermentation [currently estimated to be 80 Gt/yr (Cicerone and Oremland, 1988)] are likely to increase methane production, but this could be partially offset if diets are improved through management (Lodman *et al.*, 1993; Ward *et al.*, 1993). Methane emissions from rangeland ruminants are largely a function of intake (generally about 80% of the variance), with feed quality accounting for about 5%. Hence, increasing intake is likely to dominate the impacts of increased feed quality. However, in rangelands where feed quality is low, there is often an intake restriction (Poppi *et al.*, 1981); hence, if CO_2 and temperature reduce feed quality, there is likely to be a tradeoff betweeen reduced intake and increased emissions per

unit feed. What will happen is that the energy balance in the animal over the maintenance level will decrease, and the productivity of the animal will decrease as a consequence—and thus there will be increased methane emissions per unit product.

Global estimates of NO emissions from soils range from 4–20 Mt of nitrogen annually, representing between 16 and 20% of the global budget (Davidson, 1991; Yienger and Levy, in press). Tropical and subtropical savannas contribute almost 40% of the NO produced in soils globally, with temperate grasslands contributing another 3% (Davidson, 1991). There are no published estimates of NO production from tundras or deserts. Temperate grasslands and tropical savannas each contribute between 10 and 25% of the global N₂O budget (0.5–2.0 Mt N/yr) (Prather *et al.*, 1995).

Tropical areas that have been converted from forests to pastures due to land-use change contribute a variable proportion to both the global NO and $\rm N_2O$ budgets, with elevated emissions for many years following conversion, dropping to below original emissions after 20 years (Keller et~al., 1993). Emissions of $\rm N_2O$ from cattle and feedlots contribute an additional 0.2 to 0.5 Mt N annually. Assuming that $\rm N_2O$ emissions from pasture conversion represents as much as 50% of the emission from cultivated soils, grasslands and savannas may contribute as much as 42% of the NO emitted globally (Prather et~al., 1995).

Ammonia (NH₃) is a third nitrogen gas species exchanged with the atmosphere. Ammonia plays an important role in aerosol formation, which in turn influences radiative transfer and contributes substantially to N deposition. Approximately 50% of the NH₃ emitted to the atmosphere is produced by livestock, much of which is raised on rangelands or in feedlots, with an additional contribution by emissions from fertilizers (Dentener and Crutzen, 1994).

2.3. Ecosystem Variables

2.3.1. Herbivory

Grazing and browsing by domestic and wild animals, including invertebrates, alters the appearance, productivity, and composition of rangeland plant communities. Herbivores mediate species abundance and diversity by differential use of plants commonly susceptible to defoliation (Archer and Smeins, 1991). The role of herbivory and subsequent impacts on rangeland structure and function depends in part on the evolutionary history of grazing in an ecosystem (Payne and Bryant, 1994). Herbivory is a disturbance whether the ecosystem has a short (Milchunas *et al.*, 1988; Milchunas and Lauenroth, 1993) or long (Hobbs and Huenneke, 1992) evolutionary history of grazing.

Plant species that are well-adapted to the prevailing climate, soils, and topography may be competitive dominants of a plant community when herbivore populations are low (Archer, 1994) but may become subordinates or even face extinction as levels of herbivory increase (Archer, 1992). Grazing establishes a

new set of boundary conditions for dominance. Species with competitive advantage in a moderately grazed system are generally those that are palatable and have a capacity to sprout rapidly after being eaten. Nonpalatability becomes a competitive advantage only when grazing is excessive. For example, excessive herbivory has been shown to favor unpalatable woody species over graminoids (Archer, 1994). Examples are available from North America (Archer, 1994), Africa (van Vegten, 1983; Skarpe, 1990), northern Australia (Lonsdale and Braithwaite, 1988), and South America (Morello *et al.*, 1971; Schofield and Bucher, 1986). Browsing herbivores play a key role in maintaining grasslands, meadows, and savannas, and they can change closed woodland, thickets, or heathland into open, grass-dominated systems (Sinclair and Norton-Griffiths, 1979; Berdowski, 1987).

The extent of influence that herbivory has on the structure and function of a range system depends strongly on interactions with factors such as previous grazing history, nutrient turnover rate, fire frequency and intensity, soil moisture, and soil compaction. Studies of the interactions of vertebrate grazing with these and other factors on rangelands have illustrated the tremendous influence such interactions have on these systems (Milchunas *et al.*, 1988; Holland and Detling, 1990; Hobbs *et al.*, 1991; Holland *et al.*, 1992; Seastedt *et al.*, 1991; Parton *et al.*, 1994; Dyer *et al.*, 1993; Turner *et al.*, 1993). Invertebrate grazing, a potentially more ubiquitous and chronic factor, has received less attention but is equally important to the evolutionary and ecological organization of these systems (Evans and Seastedt, in press).

Climate change and CO₂ may also interact with grazing effects. Drought favors the concentration of herbivores at sites with more reliable water supply and hence leads to overgrazing in these locations (Heitschmidt and Stuth, 1991; Heady and Childs, 1994). Increasing CO₂ will likely result in lower forage quality because of higher C:N ratios and higher concentration of unpalatable and/or toxic compounds in plants (Fajer et al. 1989, 1991; Johnson and Lincoln, 1991). Forage consumption may increase up to a point as a result, because herbivores will need to eat more to meet nutritional demands (Fajer et al., 1991)—although the loss of palatability may reduce grazing pressure on certain species. At present, it is possible to say only that the overall carrying capacity for herbivores may increase, decrease, or remain constant, depending on the balance between eventual increases in productivity and decreases in nutritional value.

2.3.2. Fire

Fire has been a factor in the evolution of grasslands and many other rangelands. Annual net primary productivity is strongly influenced by both fire and climate (Hulbert, 1969; Old, 1969; Towne and Owensby, 1984; Abrams *et al.*, 1986; Sala *et al.*, 1988). Fire alters the structure of grassland vegetation (Knapp, 1984, 1985) and affects nutrient cycling (Raison, 1979; Kucera, 1981; Risser and Parton, 1982; Ojima *et al.*, 1990;

Ojima *et al.*, 1994a). Aboveground biomass production in temperate, ungrazed grasslands generally increases following fire during years with normal precipitation (Towne and Owensby, 1984). This increased production has been attributed to release of readily available nitrogen and phosphorus from plant material, increased nitrogen mineralization rates, enhanced nitrogen fixation, and altered microclimatic conditions, including improved light availability (Daubenmire, 1968; Old, 1969; Raison, 1979; Biederbeck *et al.*, 1980; Knapp and Seastedt, 1986; Hulbert, 1988).

By making N and other nutrients more available to soil microorganisms, fire may result in enhanced emissions of N₂O from soil (Anderson *et al.*, 1988). Bouwman (1993, 1994) calculated that from the approximately 12 Mt N/yr remaining on the ground after burning (Crutzen and Andreae, 1990), 20% is volatilized as NH₃, and 1% (0.1 Mt/yr) of the remaining N is emitted to the atmosphere as N₂O (Carras *et al.*, 1994). An estimated 10% of this N is amenable to mitigation. Most of these emissions are short-term effects, which occur directly following fire.

Grasslands subject to annual fires may suffer several long-term effects, such as decreasing soil organic matter, changes in species composition, and long-term loss of nitrogen through volatilization and immobilization (Daubenmire, 1968; Old, 1969; Biederbeck *et al.*, 1980; Kucera, 1981; Risser *et al.*, 1981; Ojima *et al.*, 1990; Ojima, 1994a). Nitrogen limitation is a common characteristic of fire-maintained grassland and rangeland ecosystems (Seastedt *et al.*, 1991).

The influence of climate change on large-scale events, such as wildfire, can only be inferred. However, the predicted increase in climate variability has led several authors to suggest that the frequency and severity of wildfires will increase in grassland/rangeland settings (Graetz *et al.*, 1988; Moore, 1990; Ottichilo *et al.*, 1991; Cherfas, 1992; Torn and Fried, 1992).

2.3.3. Land Use and Management

Land use differs from other factors influencing rangelands because of the inherent involvement of human socioeconomic factors. Human social/economic systems may produce more change in actively managed rangeland ecosystems than any other forces of global change (e.g., Burke *et al.*, 1995b). Model experiments to investigate the feedbacks between land-use change and the climate system suggest strong links (e.g., Dickinson and Henderson-Sellers, 1988).

The most common land-use transformation has been conversion of rangeland to cropland. The pattern of settlement has had important implications for rangeland transformations (Reibsame, 1990). Conventional agriculture has essentially mined many previous rangelands by enhancing decomposition, reducing soil organic matter, and increasing leaching and erosion (e.g., Bauer and Black, 1981; Burke *et al.*, 1989). The net result is that soils must now receive heavy doses of fertilizer

and pH buffers to produce acceptable yields in industrialized countries

Land use can dramatically alter C storage and fluxes, and modification of land-use practices can greatly influence the net flux of soil C, changing rangelands from a source to a sink for atmospheric C. Although conversion to small-grain cropping is not a large deviation from natural grassland ecosystems relative to albedo (except in periods of bare soil), plant stature, growing season, and energy fluxes, conversion of grasslands to cropland can result in a rapid decline in C stores. Up to 50% of soil C can be lost as a result of conversion from native rangeland to crops (Haas *et al.*, 1957; Cole *et al.*, 1989, 1990; Burke *et al.*, 1989).

For example, the potential influences of changing land management and climate-change effects on C storage of grasslands were assessed using the Century model (Ojima *et al.*, 1993b; Parton *et al.*, 1995). Future soil C pools were calculated for a "regressive management" scenario (i.e., removal of 50% of the aboveground biomass during grazed months) and a "sustainable" scenario [i.e., using moderate grazing and burning regimes as specified by Ojima *et al.* (1993b)]. The impact of "regressive" land management resulted in a loss of soil C in all regions after 50 years, with the largest losses in the warm grasslands. The total net loss relative to current condition was projected at 10.8 Gt. When this regressive management is compared to the sustainable management system (i.e., light grazing), the net difference is 37.6 Gt of soil C.

2.4. Issues of Scale

Scale is a particularly important issue in rangelands because of the very large size of management units, which is often caused by low productivity. Thus, rangeland management units incorporate spatial heterogeneity, instead of partitioning it as is usually the case in more intensive agricultural systems (Stafford Smith and Pickup, 1993). Most grasslands and rangelands are in climatic regions that are subject to frequent alterations in essential resource availability. The superimposition of management practices such as fire and grazing adds further variation in resource availability over time. Rangelands are characterized by more complex structure and function than other biomes because controlling factors (i.e., precipitation, energy, nutrients) often fluctuate rapidly over short time periods (Seastedt and Knapp, 1993). This variability in ecosystem behavior will lead to complex responses to global change.

The large areas of rangelands and the numbers of livestock they support play significant roles in biogeochemical and climate feedbacks. Response to climate change hinges on the variable scales at which these systems are used, the spatial heterogeneity incorporated in their management units, and the potentially large number of species that may interact in the primary production system (Stafford Smith, 1993). Limitations on production processes occur diurnally to seasonally through water and nutrient availability and management practices (including grazing pressure and distribution, fire, fertilizer use, and water management). Feedback effects on soils and vegetation composition,

Box 2-1. Impacts of Climate Change on Pastoral Peoples: The Example of Africa

Major shifts in climate—from relatively wet periods to dry periods or droughts—are common in the rangelands of Africa. Long-term rainfall records and other evidence from Africa's rangeland areas show that shifting climate dynamics have prevailed there for at least the last 10,000 years (Nicholson, 1983; Hulme, 1990). Traditional African livestock husbandry practices have been greatly influenced by the highly variable environment (Ellis and Swift, 1988; Behnke *et al.*, 1993; Ellis and Galvin, 1994). Because the economy depends directly and indirectly on livestock products, pastoralists have developed multiple coping mechanisms. Pastoralists cope with climate variability by keeping diverse species of livestock, by temporary emigration, by maintaining economic diversity, and even by allocating seasonal and drought-induced nutritional stress among stronger community members (Coughenour *et al.*, 1985; Galvin, 1992; Galvin *et al.*, 1994). This system requires extensive land area and external markets.

The pastoralists' stabilizing strategies have become constrained in this century primarily as a result of an increasing human population in conjunction with stable or declining livestock populations and decreasing land area. Although much recent literature suggests that livestock populations are on the increase, abundant data for the arid and semi-arid zones show otherwise. East African pastoralists have been unable to expand livestock holdings due to such factors as disease epidemics, recurring droughts, and intertribal raiding (Sandford, 1983; Homewood and Rodgers, 1984; O'Leary, 1984; Arhem, 1985; Sperling, 1987; McCabe, 1990). In addition, dry-season ranges with more reliable water supply have been lost to colonial and African agriculturalists, to game parks, and to game conservation areas (Campbell, 1984; Bekure *et al.*, 1987; Homewood *et al.*, 1987; Little, 1987). Pastoralists also have taken up agriculture in an effort to meet their increasing food demands. Thus, with increasing population pressure on a declining resource base, there is an expanding reliance on the marketing of animals. However, African livestock market infrastructure and stability is still in an early stage of development.

Persistence of the pastoralists' system in the arid and semi-arid ecosystems of Africa will require a clear understanding of the nonequilibrium dynamics of these systems and development of additional coping strategies.

including carbon and nitrogen sequestration, are thus influenced at seasonal, annual, and decadal temporal scales, but are experienced at landscape spatial scales.

2.5. Extreme Events

Increased frequency and magnitude of extreme events is often mentioned as a potential characteristic of future global climate (Easterling, 1990). Because extremes drive rangeland systems (Griffin and Friedel, 1985; Westoby et al., 1989), small changes in the frequency of extreme events may have a disproportionate effect on what management must cope with in these systems. For example, the structure of long-lived perennial communities may change drastically if the frequency of extremes increases significantly, because seedling establishment and mortality of these plants are highly sensitive to extremes (Graetz et al., 1988). Both the stability of forage supply and the balance between temperate and subtropical species are largely controlled by the frequency of extreme climatic events and thus are subject to change in a CO₂-warmed world (Campbell and Grime, 1993). Individual events (e.g., a major rainfall event that recharges deep moisture stores) and extended periods of above- or below-average temperature or rainfall are both likely to be significant (Stafford Smith and Morton, 1990).

Rangelands are systems adapted to a wide range in climate, fire frequencies, and grazing intensities, but anthropogenic fragmentation has already affected rangeland systems such that many systems may be vulnerable to further pressures (Archer, 1994). With the addition of climate change to existing impacts, rangelands may be more susceptible to extreme events such as drought, 100-year floods, and insect outbreaks.

2.6. Boundary Changes

Boundaries among rangeland vegetation types and between rangeland systems and other biomes are likely to change with changes in climate. Shifting boundaries between plant community types (the ecotone), potentially in response to past changes in climate, are well documented in the fossil record (Solomon and Shugart, 1993). Significant changes in the distribution of grasslands and arid lands worldwide in response to climate change are suggested by biogeographical models (Emanuel et al., 1985; Prentice and Fung, 1990; Prentice et al., 1992; Neilson, 1993; Henderson-Sellers and McGuffie, 1995). Specific changes in rangeland ecosystem boundaries will be determined by the nature of climate change, including the frequency and severity of extreme events. As nonequilibrium systems, rangelands may experience structural reorganization, and individual species may change distribution, but there probably will not be any synchronized movement of entire vegetation belts. Land-use change and human interventions will greatly modify the expressions of climate change and may overwhelm them, particularly in tropical and subtropical areas (Parton et al., 1994).

Semi-arid and arid ecosystems may be among the first to show the effects of climate change (OIES, 1991). Their sensitivity to climate change may be due to the current marginality of soil water and nutrient reserves. The droughts of the 1930s and the 1950s in the United States, for example, changed plant production systems (Weaver and Albertson, 1944; Albertson *et al.*, 1957) and led to modification of land surface characteristics. Weaver and Albertson (1944) showed that the distribution of grasslands changed in the United States, with the shortgrass species moving eastward into the midgrass prairie and midgrass species moving eastward into the tallgrass prairie. In addition, these grasslands were invaded by ruderals (weedy species) and other non-native grasses. In Australia, the distribution of *Heteropogon contortus* shifted west in wet decades and eastward in drier periods (Bisset, 1962).

The balance between herbaceous and woody vegetation is sensitive to climate in most grassland/savanna regions (Parton *et al.*, 1994). Changes such as replacement of grasses with woody plants can occur quite quickly (Griffin and Friedel, 1985; McKeon *et al.*, 1989; Westoby *et al.*, 1989)—within a decade or so in response to a mixture of reduced grazing, fire suppression, and climate variability. Fire and grazing regimes, in conjunction with changes in climate characteristics affecting soil moisture status, relative humidity, or drought stress, will have the greatest influence on grassland-woody species boundaries (Neilson, 1986; Hulbert, 1988; Schlesinger *et al.*, 1990; Hobbs *et al.*, 1991; Archer *et al.*, 1995).

Mayeux et al. (1991) discuss evidence that open, mostly C₄ grasslands worldwide are becoming increasingly populated by C₃ woody plants—a process abetted, perhaps, by the 25 to 30% increase in atmospheric CO₂ and correlated rise in plant WUE in the last two centuries. There is ample evidence that C₃ woody species have increased in both mesic and arid C₄ grasslands during the historical period of CO₂ increase. The change from shrubland to grassland that would be predicted from climatic diagrams as plant water-use efficiency rose, however, has not been evident. Here, the opposing influence of a possible change to a warmer, drier climate since industrialization—perhaps in combination with grazing by domestic livestock (Hastings and Turner, 1965; Archer et al., 1995)—may have negated the effects of increased CO₂ on vegetation structure.

In some regions, warmer temperatures and increased summer rainfall, with fewer frost days, may facilitate the encroachment of both annual and perennial subtropical C₄ grasses (e.g., *Digitaria sanguinalis*, *Paspalum dilatatum*) into some temperate C₃ grassland areas. This would likely cause a depression in forage quality and result in a more pronounced warm-season peak in biomass production, with consequent problems for traditional livestock systems. The rate of invasion of these and other weed species is expected to be greatest in more productive grassland and rangeland systems, with high stocking pressures, high utilization, and consequently greater opportunities for seedling establishment and invasion in gaps (Campbell and Hay, 1993; Campbell and Grime, 1993). The invasion rates of C₄ grasses may be offset to some extent by increased atmospheric CO₂ concentration (Campbell and Hay, 1993), but the effects are unclear.

Biogeographical shifts predicted for CO_2 and temperature increases are variable, depending on the vegetation classification used, general circulation model (GCM) assumptions, and assumptions about current vegetation distribution and equilibrium status (Parton *et al.*, 1994). Recent analyses using BIOME 1.1 (Prentice *et al.*, 1992) and IMAGE 2.0 (Alcamo, 1994) were compared to determine potential rangeland boundary shifts under different model assumptions (Table 2-3; see also Chapter 1, Figures 1-3 through 1-7, and Table 1-2).

The results suggest that rangelands are likely to be vulnerable to biogeographic change and that the areal extent of the changes may be significant (Table 2-3). Warm grass/shrub types will likely expand, while tundra ecosystems will most likely contract. The opposing results occur because of differences in the definitions of vegetation types, regional variation, and model assumptions. However, the analysis is instructive.

The direction of carbon-storage changes projected by three GCM models of climate change do agree quite closely under

Table 2-3: Potential changes in extent of rangeland cover types from the BIOME 1.1 model (Prentice et al., 1992) and IMAGE 2.0 (Alcamo, 1994). Numbers are in 10⁶ km² and are rounded, so numbers do not exactly sum.

	_	BIOMI O ₂ (G	_	IMAGE 2.0 (TVM) 2050			
Туре		A ²		B^1	A ²	C^3	
Cool Semi-Desert	4.91	2.61	-2.30	2.28	2.28	0.00	
Cool Grass Shrub	7.17	3.91	-3.21	5.26	8.12	2.85	
Warm Grass Shrub	9.84	17.92	+8.08	17.50	25.98	+8.48	
Hot Desert ⁴	20.70	20.90	+0.199	16.90	16.46	-0.44	
Tropical Savanna/ Dry Woodland	17.18	19.79	+2.61	11.46	3.68	-7.79	
Xerophytic Wood/ Shrubland	10.63	11.89	+1.25	8.50	4.69	-3.81	
Tundra	11.61	4.40	-7.21	11.38	11.34	-0.04	

Note: This table does not display which vegetation types specifically change into another vegetation type. Refer to Figures 1-3 through 1-7 and to Table 1-2 in Chapter 1 for a graphical display of changes in rangeland boundaries between types.

Source: Rik Leemans, RIVM, The Netherlands.

climate-change scenarios (Table 2-4). Analyses indicate that carbon stores are expected to increase in warm grass shrub and tropical savanna/dry woodland types, partly because these vegetation types are expected to expand (Solomon *et al.*, 1993). Conversely, total carbon stores are likely to decline in the other major rangeland types.

It is important to compare these impacts to those resulting directly from human activity (Parton *et al.*, 1994). According to Burke *et al.* (1990), the impact of a 2 x CO₂-driven climate-change scenario on grassland soil C levels in the southern Great Plains would be an order of magnitude smaller than the impact of plowing the grassland for crop production. Mosier *et al.* (1991) have shown that plowing and fertilization of grasslands increases N₂O flux by 50% and decreases soil sink strength for CH₄ by 50%. These impacts, too, are much larger than the potential effects of a 2 x CO₂-driven climate change (Burke *et al.*, 1990). While the effects of plowing on soil carbon and trace-gas fluxes may be large on a regional basis, the impact of CO₂ and climate may be similar on a global average. The effects of climate and land-use changes combined could lead to more rapid changes than either would alone.

2.7. Regional Variation

2.7.1. Low-Latitude Regions

Natural tropical grasslands (Box 2-2) are a close second to tropical forests in extent and may equal them in productivity (Hall and Scurlock, 1991). Tropical grasslands and savannas are important as both a source and a sink of C at the regional and world level. Because of their extent, productivity, and capacity for above- and belowground biomass accumulation, the amount of C sequestered is very high (Fisher *et al.*, 1994), (Tables 2-2 and 2-4). On the other hand, they are frequently burned and therefore represent a large efflux of C into the atmosphere. Almost one-fifth of the world's population lives in these ecosystems, many in rural societies that depend on subsistence agriculture (Frost *et al.*, 1986).

Extreme events seem to influence the system more strongly than do average climatic parameters. Highly seasonal water availability and chronically low soil-nutrient availability appear to be the most limiting factors (Medina, 1982; Frost et al., 1986; Solbrig et al., 1992). Natural and anthropogenic fires are a major and apparently very ancient structuring force. In some tropical systems, frequent burning does not lead to major changes or invasion, and the dominants tend to recover fast (Coutinho, 1982; Farinas and San José, 1987; Lewis et al., 1990; Medina and Silva, 1990; Silva et al., 1991). In others, invasion of exotic species is the norm (D'Antonio and Vitousek, 1993). The effect of climate change on tropical rangelands will depend on the balance between increasing aridity favoring C₄ grasses and increasing CO₂ concentration favoring C₃ photosynthesis (Box 2-3). The already low nutritional value of most tropical grassland plants may decrease as a consequence of increased C:N ratio and because of higher

 $^{^{1}\,}B=$ Before climate change; numbers vary because of different assumptions used in the classification of vegetation types between the models.

 $^{^{2}}$ A = After climate change.

 $^{{}^{3}}C$ = Change in area.

⁴See Chapter 3.

Box 2-2. The Northern South America Savanna

Location: Northern South America (Medina, 1986, 1987; Sarmiento, 1983, 1984; Sarmiento and Monasterio, 1983; Goldstein and Sarmiento, 1987).

Climate: Average daily temperatures ranging from 22°C to more than 35°C; average annual precipitation ranging from 800 to 2000 mm with a strong seasonal distribution, including a dry period of 3–6 months (Medina, 1982; Sarmiento *et al.*, 1985).

Vegetation: Continuous cover of perennial grasses with a significant discontinuous cover of perennial woody plants (Medina, 1982; Medina and Silva, 1990).

Probable biological impacts of climate change: An alteration in the amount and pattern of rainfall, the occurrence of extreme events (e.g., hurricanes, drought), and the El Niño–Southern Oscillation (ENSO) may alter actual functioning of savanna ecosystems. The vegetation structure of the ecosystems located at higher altitudes may become similar to those 300–500 m lower in elevation. During ENSO years, precipitation in northern South America is lower (Aceituno, 1988), increasing the likelihood of drought. Because ENSO events could become more frequent and bring more severe weather under a doubled-CO₂ climate, these systems could fail to function as they do now.

production of secondary metabolites in C_3 plants (Oechel and Strain, 1985; Fajer *et al.*, 1989). Thus, the carrying capacity for herbivores may be reduced in this region.

2.7.2. Middle-Latitude Regions

Temperate rangeland systems experience drought stress at some time during the year, but the degree of drought stress and its timing vary among regions. The distribution of different rangeland types is correlated with different climatic patterns, including the seasonal distribution of mean monthly air temperature and precipitation and the ratio of precipitation to potential evapotranspiration (e.g., see Boxes 2-4 and 2-5).

Temperate grasslands and associated savannas and shrublands clearly are vulnerable to climate change. Parton *et al.* (1993) highlight three ways in which changing climate might influence

mid-latitude grassland ecosystem function and structure. In some grassland regions, significant reductions in precipitation or increases in temperature may accelerate degradation and lead to the replacement of grassland vegetation by woody species. Second, soil erosion rates may increase as plant cover decreases, leading to a nearly irreversible loss of productive potential. Finally, the above transitions are almost always exacerbated by intense human land use, as occurs in most temperate grassland and savanna regions (OIES, 1991; Archer *et al.*, 1995). Degradation can thus occur through both functional (e.g., reduced primary productivity) and structural (e.g., perennial-to-annual vegetation, shrub encroachment) change (see Boxes 2-6 and 2-7).

Nutrient cycling in temperate grasslands is largely driven by climate. Rates of carbon gain, decomposition, and nutrient cycling are all sensitive to temperature and moisture (Parton *et al.*, 1987; Schimel *et al.*, 1990). Soil organic-matter storage—the primary

Table 2-4: Rangeland BIOME 1.1 carbon stocks (in Gt) under three 1994 IPCC (Greco et al., 1994) climate scenarios (Max-Planck Institute, Geophysical Fluid Dynamics Laboratory, and UK Meteorological Office). Data are from Solomon et al., 1993; current carbon estimates can be found in Table 2-2.

Туре	ECI AG ¹	HAM Cl BG ²	imate C ³	G ¹	FDL Clin BG ²	mate C ³	UK AG ¹	MO Cli BG ²	mate C ³
Cool Semi-Desert	2.1	21.5	-10.2	1.7	17.6	-14.4	1.5	15.7	-16.5
Cool Grass Shrub	4.1	50.2	-22.3	3.2	39.3	-34.1	2.4	29.5	-44.7
Warm Grass Shrub	17.4	116.7	+33.8	19.7	132.1	+51.6	22.5	150.3	+7.2
Hot Desert	6.2	62.4	-0.8	6.3	63.5	-5.9	6.2	61.7	-1.5
Tropical Savanna/Dry Woodland	75.9	120.4	-7.1	91.5	145.2	+33.3	99.0	157.1	+52.7
Xerophytic Wood/Shrubland	47.1	83.9	+4.6	44.4	79.1	-2.8	46.5	82.7	+2.8
Tundra	4.4	100.8	-34.7	3.3	76.0	-60.6	2.4	55.2	-82.2

 $^{{}^{1}}AG = Above$ ground biomass from current climate estimates.

²BG = Below ground biomass from current climate estimates.

³C = Change in total carbon stocks (Gt) from current climate estimates.

Box 2-3. African Savannas

Location: Nearly continuous distribution in the central African continent (see Figure 2-1).

Climate: Distinct wet (600–1500 mm/yr) and dry (400–800 mm/yr) savannas.

Vegetation: Distinct layers of woody and herbaceous vegetation. In the moist savanna, vegetation is dominated by broad-leafed trees of the genera *Brachystegia* and *Julbernadia* as dominants. Herbivory by large mammals consumes a relatively small fraction of total primary production (5–10%) due to high concentrations of secondary compounds (mainly tannins) and low nitrogen concentrations in the foliage of the woody plants; thus, there is a high fire-fuel load and a short (1–3 year) fire interval. Dry savanna is dominated by fine-leafed trees (mainly *Acacia*) and stoloniferous grasses (Scholes and Walker, 1993). Large mammal herbivory is high (10–50% of total primary production), the fuel load is low, and the inter-fire interval is relatively long (5+ years).

Probable biological impacts of climate change: The major predicted impact is an increase in the frequency and severity of drought (McKeon *et al.*, 1993). An increase in the frequency of drought is likely to lead to episodic die-offs of woody vegetation. This will increase the fire-fuel load and thus potentially increase the frequency and intensity of fires. The greatest impacts are likely to be in the semi-arid savannas, where human populations depend mainly on pastoralism (see Box 2-1). Human responses are likely to include increasing the distribution and security of surface water for live-stock. This is likely to further weaken the grass layer, with acceleration of desertification. One strategy to bolster the production of animal protein would be to promote the sustainable use and management of indigenous herbivore species, especially preferential browsers (giraffe, eland, kudu, impala, etc.), many of which are independent of surface water and largely do not compete with domestic grazers.

reserve for nutrients in grasslands—is sensitive to temperature and generally decreases with increasing temperature. In New Zealand, research using both spatial analogue (Tate, 1992) and modeling approaches (Tate *et al.*, 1995) has shown that soil carbon could decline by about 5% per °C increase in regional temperature. If temperatures increase in grasslands worldwide, soil carbon storage is likely to decline (Parton *et al.*, 1994). Declining soil carbon would likely lead to nutrient loss in the longterm, and could lead to degraded hydrological properties and increased

erosion. Losses of soil carbon and increases in temperature could also lead to higher trace-gas emissions as the soil N-cycle is accelerated. Thus, carbon storage and nutrient cycling in temperate grasslands could change significantly if climate changes; indeed, interannual variability in climate is clearly reflected in observed and modeled production and decomposition. However, Buol *et al.* (1990) showed that, for soils that experience a wide annual temperature fluctuation, there is no correlation of organic carbon content to mean annual temperature.

Box 2-4. Rio de la Plata Grassland in South America

Location: Argentine Pampas, the Campos of Uruguay, and Southern Brazil.

Climate: Temperate humid to semi-arid. Mean annual temperature 13–18°C, mean annual minimum temperature <13°C. Mean annual rainfall 400–1600 mm, evenly distributed over the year in the east, becoming concentrated in spring and fall in the west (Cane, 1975; Cabrera, 1976; Lemcoff, in Soriano, 1992).

Vegetation: Mostly tall tussock grasses, but perennial grazing lawns are the actual physiognomy. C_3 and C_4 grasses, with the growth of C_3 and C_4 grasses segregated temporally (Cabrera, 1976; Arana *et al.*, 1985; Leon, in Soriano, 1992).

Probable biological impacts of climate change: These grasslands are vulnerable to drought. IPCC climate scenarios (Greco *et al.*, 1994) suggest that mean annual winter (JJA) temperatures may increase 0.5 to 1°C, while mean annual summer (DJF) temperatures may increase as much as 2°C. Generally summer (DJF) precipitation is expected to decline from 0–40% by the year 2050, while winter (JJA) precipitation may increase or decrease $\pm 20\%$ in the region (Greco *et al.*, 1994). If these projections are correct, the crop and animal production for the region could drop drastically. During the 1920s and 1930s, extremely dry conditions caused a shift of agriculture to the east, and the abandoned agricultural land eroded, with the loss of 60,000 km² of arable land (Suriano *et al.*, 1992). Unusually dry summers may bring about some long-lasting changes in community structure (Chaneton *et al.*, 1988; Sala, in Soriano, 1992). The projected changes may allow C_4 species to develop earlier in the season, while decreased summer precipitation will likely favor C_3 species.

Box 2-5. Mediterranean-Basin Region

Location: Bordering the Mediterranean Sea, stretching 5000 km eastward from the Atlantic coast between 30 and 45°N.

Climate: Transitional between temperate and dry tropical climates, with a distinct summer drought of variable length. Highly variable annual precipitation.

Vegetation: Evergreen sclerophyllous shrubs that change to heathlands in nutrient-poor soils along an increasing-moisture gradient and into open woodlands and annual grass or dwarf shrub steppes along an increasing-aridity gradient.

Probable biological impacts of climate change: A shift of carbon storage from soil to biomass is likely to occur, with probable negative effects on soil stability and increased erosion (Ojima *et al.*, 1993b). Mediterranean rangelands are expected to undergo a 300–500 km poleward extension of grass and dwarf shrub steppes at the expense of the sclerophyllous shrubland. In Euro-Mediterranean countries, extension of shrubland as a result of agricultural release is expected, with a parallel increase in wildfires and evapotranspiration, and a decrease in livestock grazing with increases of game and other wildlife. In Afro-Asian Mediterranean countries, extension of agriculture and overgrazing in marginal areas, combined with overall smaller P:PET ratios, will probably lead to further degradation of plant cover and soil loss.

Finally, the balance between herbaceous and woody vegetation is sensitive to climate in most grassland/savanna regions, and the productivity and human utility of these systems is very sensitive to this balance (see Boxes 2-5 through 2-8).

2.7.3. High-Latitude Regions

Warming is expected to be most pronounced at the poles (Spicer and Chapman, 1990; Long and Hutching, 1991). In the high southern latitudes of South America, annual mean temperature and low and irregularly distributed precipitation (especially as ice and snow) are the main factors constraining grassland productivity (Mann, 1966; Sala *et al.*, 1989; Fernández-A. *et al.*, 1991). Most Southern Hemisphere high-latitude

grasslands lie to the south of the 13° C isotherm and are composed of C_3 species. By 2050, virtually all Southern Hemisphere grasslands might lie to the north of that isotherm; thus, the area would be more suitable for C_4 species (R. Rodríguez and G. Magrin, pers. comm., on the basis of Deregibus, 1988). This change in species composition would decrease the nutritional value of the grasslands, further decrease their carrying capacity, and eventually aggravate the overgrazing-erosion problem. On the other hand, dominant C_3 grasses and shrubs may be promoted by elevated CO_2 , depending on water availability, and the increased growth may eventually lead to increased production and carrying capacity.

Indirect temperature effects associated with changes in thaw depth, nutrient availability, and vegetation will cause substantial

Box 2-6. Great Basin of North America

Location: Nevada and rain-shadow parts of Oregon, California, Utah, and Arizona in the United States.

Climate: Continental climate with average annual precipitation averaging 50–250 mm. Snow and hard frost are common in winter.

Vegetation: The Great Basin desert is dominated by big sagebrush (*Artemesia tridentata*), although other shrubs dominate on shallow saline soils (*Atriplex* sp.) or in specific soil complexes. Cover is generally low, varying from 5 to 50%.

Some probable biological impacts of climate change: There are a number of possible vegetation changes that could occur as a result of IPCC climate-change scenarios. An increase in precipitation during the growing season may increase the proportion of grasses and forbs over woody plants, which may increase the potential for more frequent fires, further favoring grasses. Cold conditions with increased precipitation during the winter will likely favor drought-tolerant woody species (e.g., *Artemisia* sp.) over herbaceous species. These conditions would also decrease fire frequency, thereby benefiting woody plants over grasses and forbs. Mild, wet winters and dry summers may enhance the spread and dominance of introduced Eurasian annuals such as cheatgrass (*Bromus tectorum*) and Russian thistle (*Salsola kali*). Cheatgrass is a fire-prone species, and previous work has demonstrated that frequent fire-return intervals occur with cheatgrass dominance (Whisenant, 1990). A decrease in total annual precipitation will likely result in shrub steppe communities shifting toward desert shrub.

Box 2-7. European Steppe and Semi-Natural Grassland

Location: Scattered throughout Europe.

Climate: Steppes occupy sites with a continental climate and annual rainfall between 350–500 mm concentrated in the warm season, but with late-summer drought (Walter, 1968). Semi-natural grasslands occupy a wide range of climates, with annual rainfall between 400 mm and 2300 mm (Titlyanova *et al.*, 1990).

Vegetation: Steppes are multi-layered communities (Lavrenko and Karamysheva, 1992), with tall bunch grasses (*Stipa* sp.), short bunch grasses (*Cleistogenes* sp., *Festuca* sp.), and dwarf bunch species (*Carex* sp., dwarf *Stipa* sp.); moss layers are dominant in the northern zone, and ephemeral plants plus lichen layers are dominant in the southern zone. Seminatural grasslands are secondary plant communities with a multi-layer structure of grasses and forbs (Rychnovska, 1992). Floristic diversity provides semi-natural grasslands better potential adaptation to climate fluctuations; belowground biomass and soil aggregation are the main stabilizing factors.

Probable biological impacts of climate change: Increases of $3 \pm 1.5^{\circ}$ C within the next century as projected in current scenarios (Greco *et al.*, 1994), could cause a 250–300 km northern displacement of phytoclimatic boundaries (Anderson, 1991) with a substantial reduction of tundra, mires, and permafrost areas and a parallel expansion of grassland and grain cropping into the southern margin of boreal forest zones in Europe. In addition, changes in the concentration of atmospheric gases may alter the competitive relationships in the plant community. For example, indirect competitive effects have been reported in southern Britain (Evans and Ashmore, 1992), where above-normal ozone concentrations caused a decrease in the biomass of upper-layer dominant grasses with a parallel increase in lower-layer forb biomass by reducing competition for light.

changes in Arctic species composition, litter quality, and nutrient availability (Chapin and Shaver, 1985; Oberbauer and Oechel, 1989; Kielland, 1990; Marion *et al.*, 1991; Nadelhoffer *et al.*, 1991; Havstrom *et al.*, 1993; Wookey *et al.*, 1993; Chapin *et al.*, 1995). Increased nutrient availability increases shrub abundance and decreases the abundance of mosses, an important soil insulator (Chapin *et al.*, 1995).

The changes in biotic interactions that will occur with climatic warming are poorly known. Field experiments of ≤10 years duration, simulating a 3°C warming, show an increase in shrub abundance and a decline in species richness (Chapin *et al.*, 1995). Insect-pollinated forbs are expected to decline—suggesting that insect pollinators (Williams and Batzli, 1982) and migrating caribou, which utilize these forbs during lactation, could be adversely affected (White and Trudell, 1980). Warmer summers also increase insect harassment of caribou and cause declines in feeding and summer energy reserves. In contrast, browsing mammals, such as snowshoe hare and moose, may benefit from climatic warming because an increase in shrubs will increase fire frequency and lead to an increase in the proportion of early-successional vegetation.

The presence of trees at high latitudes may be determined more by soil temperature than by air temperature (Murray, 1980), so expected warming of soils and increase in thaw depth could have a strong influence on treeline location. Simulation models suggest that conversion of boreal forest to a treeless land-scape would increase winter albedo, reduce energy absorption, and cause a 6°C decrease in regional temperature (Bonan *et al.*, 1992). Conversely, we expect treeline advance to provide a strong positive feedback to regional and global warming.

Regional warming and treeline advance are expected to increase fire frequency, directly releasing CO₂ stored in peat to the atmosphere. Current predictions (Anderson, 1991) indicate that the tundra may change from being a sink to a source of C, with a net flux to the atmosphere of about 100 g C/m⁻²/yr. This study also projected that about 15% of C storages in soils of peats, tundra, and boreal forests could be released over the next 50 years. Recent work suggests soil drying over the past decade (Maxwell, 1992) has already changed the Alaskan tundra from a net sink to a net source of CO₂ (Anderson, 1991; Oechel *et al.*, 1993; Zimov *et al.*, 1993a, 1993b).

2.8. Modeling Rangeland Ecosystem Response

Several models are currently used to predict rangeland response to climate change and land use. While most global-scale models are correlational—such as those based on the Holdridge Life Zone classification scheme (e.g., Emanuel *et al.*, 1985)—there are many regional-scale models of ecosystem dynamics in rangelands (e.g., Century: Parton *et al.*, 1987, 1988, 1994; GEMS: Hunt *et al.*, 1991; GRASS: Coughenour, 1984; Hurley model: Thornley and Verbene, 1989; Thornley *et al.*, 1991; SPUR: Hanson *et al.*, 1993; STEPPE: Coffin and Lauenroth, 1990; GRASP: McKeon *et al.*, 1990).

These models generally show that when a variety of directional climate change scenarios are imposed on rangeland ecosystems, such as in Century model simulations, effects are detectable but small on a per-unit-area basis relative to changes induced by management activities (Burke *et al.*, 1989)—although climate effects are more substantial globally (Parton

Box 2-8. Australian Tussock Grassland and Steppe

Location: Alluvial plains running southwest from the eastern half of the continent.

Climate: There is an enormous climatic gradient across the continent, from 100–200 mm median annual rainfall in the central part of the region—distributed throughout the year at random, without seasonality—to 800–900 mm along the northern and southern borders, the former concentrated in summer and the latter in winter as a Mediterranean-type climate. In the south, there are a significant number of frosts; winter rains are usually gentle and associated with frontal systems passing around the South Pole. In the north, there is no frost, and rains are often monsoonal and very heavy. Occasionally, northern cyclonic incursions may reach the south, bringing the heaviest rainfall events. Rainfall variability is very high—increasing toward the equator and as annual totals decline—and is greatly affected by ENSO and other climatic systems driven by sea surface temperatures in the Pacific and Indian oceans.

Vegetation: A complex range of communities, including monsoon tallgrass (*Schizachyrium* sp.), subtropical and tropical tallgrass (*Heteropogon contortus*), tussock and midgrass (*Astrebla* sp., *Aristida* sp., *Bothriochloa* sp.), hummock grasslands (*Spinifex* sp.), acacia and eucalyptus shrublands and woodlands, temperate grasslands (*Themeda triandra*, *Danthonia* sp.), annual grasslands (*Echinochloa* sp.), and chenopod shrublands (*Atriplex* sp., *Maireana* sp.).

Probable biological impacts of climate change: Scenarios of future climate (Greco *et al.*, 1994) suggest increased variability and unpredictability in productivity and community composition in the region (McKeon and Howden, 1991; Stafford Smith *et al.*, 1995). A shift toward summer rainfall will have a major effect in southern Australia, where vegetation is currently dominated by winter rainfall (Stafford Smith *et al.*, 1995). Although it is unlikely that mean climatic conditions will move outside their envelope of current possible conditions, extreme drought periods, high intensity rainfalls, and water distribution could become more common (Whetton, 1993; Stafford Smith *et al.*, 1995).

et al., 1995). A recent intercomparison of several of these models showed that the degree to which forests invade grasslands or vice versa depends on the GCM climate scenario used (VEMAP Participants, 1995).

These models, plus recent global-scale mechanistic models, have been used to evaluate the outcome of various management schemes, including fire, grazing, and strip-mine reclamation (e.g., de Ridder *et al.*, 1982; Coughenour, 1984, 1991; Coffin and Lauenroth, 1990; Ellis *et al.*, 1990; Ågren *et al.*, 1991; Hunt *et al.*, 1991; Holland *et al.*, 1992; Hanson *et al.*, 1993; Ojima *et al.*, 1994b). They have also been used to assess potential impacts of various climate scenarios on plant productivity and nutrient cycling (e.g., BIOME-BGC: Running and Hunt, 1993; Century: Parton *et al.*, 1987, 1992, 1994; SPUR: Hanson *et al.*, 1993; TEM: McGuire *et al.*, 1992).

Results from tests of rangeland sensitivity to climate and management using these models support previous discussion of the importance of seasonality and distribution of rainfall, and suggest that rangelands are sensitive to changes in environmental conditions associated with fire and grazing as well as their land-use history.

2.9. Human Adaptation

By the time there is a detectable rise in mean temperature of a degree or two, pastoral societies may already have begun to adapt to the change. Adaptation may be more problematic in some pastoral systems where production is very sensitive to climatic change, technology change is risky (Caceres, 1993), and the rate of adoption of new technology is slow. Decreases in rangeland productivity would result in a decline in overall contribution of the livestock industry to national economies. This would have serious implications for the food policies of many underdeveloped countries and on the lives of thousands of pastoral peoples.

Intervention—in terms of active selection of plant species and controlled animal stocking rates—is the most promising management activity to lessen the negative impact of future climate scenarios on rangelands. Proper rangeland management, including sustainable yield and use of good-condition areas while marginal or poor condition areas are allowed to rest, will become increasingly necessary under climatic conditions projected for the future. A shift in reliance toward more suitable and more intensively managed land areas for food and fiber production could have the dual benefits of greater reliability in food production and lesser detrimental impact of extreme climatic events such as drought on rangeland systems. Improvement and intensification of management of certain areas of rangeland may also have the additional benefit of reducing average methane emissions per head of livestock because of improved feed quality.

One management option for the future is to actively change species composition of selected rangelands. Legume-based grassland systems may become more important in the future because legumes reduce the reliance on fertilizer inputs and improve the nutritive value of forage. The use of leguminous species is important as a means of producing more-sustainable forage systems (Riveros, 1993). Legume species generally show larger yield responses to elevated CO₂ than do grasses at warm temperatures and also show enhanced nitrogen-fixation rates (Crush *et al.*, 1993; Newton *et al.*, 1994; Campbell *et al.*, 1995a). The benefits of leguminous species could be offset to some extent by future increases in damaging UV-B radiation (Caldwell *et al.*, 1989), because legumes may be quite susceptible to UV-B relative to other species (Krupa and Kickert, 1989; Brown, 1994). However, the effects are uncertain at present because there are only limited experimental data available on the effects of future UV-B radiation levels on forage and rangeland legumes.

In some grass-dominated rangeland systems, improved pastures may help people to adapt livestock grazing strategies. In these systems, there is significant intervention—including selection of forage type, selective animal breeding, pasture renewal, irrigation, and other practices (Campbell and Stafford Smith, 1993). This intervention provides opportunities for graziers to adapt systems so they are protected against negative effects of global change and so that any potential benefits are realized. McKeon *et al.* (1993) developed a scheme for adapting rangelands to climate change by linking management decisions to climate variability.

2.10. Mitigation

Opportunities for reducing greenhouse gas (GHG) emissions on rangelands (Table 2-5) include maintaining or increasing carbon sequestration through better soil management (Ojima *et al.*, 1994b), reducing methane production by altering animal-management practices (Cicerone and Oremland, 1988; Howden *et al.*, 1994), and using sustainable agriculture practices on rangelands capable of sustaining agriculture (Mosier *et al.*, 1991).

Productivity and carbon cycling in rangeland ecosystems are directly related to the amounts and seasonal distribution of precipitation and are only secondarily controlled by other climate variables and atmospheric chemistry (Sampson *et al.*, 1993). In fact, rangeland productivity may vary as much as fivefold because of timing and amounts of precipitation (Walker, 1993).

Carbon storage in grasslands, savannas, and deserts is primarily below ground (Table 2-2). Estimates using the BIOME model (Solomon *et al.*, 1993) suggest that in the world's rangelands approximately 595 Gt C is stored in belowground biomass (44% of the world's total), while only about 158 Gt is stored in rangeland aboveground biomass. Thus, good soil management is the key to keeping or increasing C storage and protecting rangeland health (condition). Improving rangeland health, and thus the amount and kind of vegetation, will also reduce methane emission from ruminant animals per unit product by improving the quality of their diet. Total methane emissions from the grazing system will decrease only if there are commensurate reductions in animal numbers in the less-resilient parts of the grazing land-scape however (Howden *et al.*, 1994).

Nonsustainable land-use practices such as inappropriate plowing, overgrazing by domestic animals, and excessive fuelwood use are root causes of degradation of rangeland ecosystems (Ojima *et al.*, 1993b; Sampson *et al.*, 1993). Some systems may already be degraded to such an extent that the ability of the ecosystem to recover under better management practices will be greatly hampered. Practices listed in Table 2-5 may prove to be useful in GHG mitigation. None of the practices is relevant for every country, social system, or rangeland type. Unfortunately, because of the high dependence of rangeland function on adequate amounts and timing of rainfall, none of these practices is likely to significantly improve rangeland function and carbon sequestration without adequate rainfall (Heady, 1988; McKeon *et al.*, 1989).

Reduction of animal numbers. Reduction of animal numbers can increase carbon storage through better plant cover (e.g., Ash et al., 1995) and decrease methane emissions. This practice can have a positive ecosystem effect if there is sufficient rainfall, but reduction in animal numbers on rangelands may require alternative sources of food for humans, and thus changes in national and/or regional food-production policies.

Changing the mix of animals. Changing the mix of animals on a given rangeland area can increase carbon storage and decrease methane emissions, but the benefit derived depends on the kind of rangeland and the proposed mix of animals. If a country is considering only cattle and small stock (sheep, goats, etc.), the mix may not be ecologically efficient; rather, it may reflect an economic risk aversion—in bad times, cattle die but goats survive. In this kind of grazing mix, the ecosystem may deteriorate. In contrast, a mix of cattle and wildlife ruminants may be both ecologically and economically efficient.

Changing animal distribution. Changing animal distribution through salt placement, development of water sources, or fencing can increase carbon sequestration through small increases in plant cover overall and improved status of the root system (due to less intense grazing). None of the changes in animal distribution, however, is expected to affect methane production. Animal-management practices will be specific to local and regional production systems; for example, fencing and/or placement of salt may not be useful in herding systems and may potentially interfere with wildlife migration. Costs and practices will vary widely by region.

Agroforestry. In regions where woody species and grasses coexist (Boxes 2-2, 2-3, 2-5, and 2-8), management practices to enhance both woody and herbaceous productivity may increase carbon storage and reduce methane emissions per unit product from domestic and wild ruminants, by improving the quality of the diet.

Watershed-scale projects. Practices involving the development of dams with large-scale water-storage capacity may improve long-term carbon storage and reduce animal methane production per unit product, by improving the quality of the diet through improved animal-management options and improved

Table 2-5: Practices (mitigation options) to improve rangeland condition or health, and to reduce GHG emissions on rangelands. Possible effects of implementing each practice are listed for two greenhouse gases, and qualitative cost/benefits estimates are provided. Unhealthy, poor-condition rangelands are those lands where soil loss, plant species and cover loss, species invasions, and interrupted and poorly functioning nutrient cycling are the norm. Good condition, healthy rangelands, on the other hand, have nutrient cycling and energy flows intact; soils are not eroding; and plant species composition and productivity is indicative of a functioning ecosystem (NRC, 1994).

Practice	Healthy	Not Healthy	Carbon	Methane	Biophysical Benefit/Cost	Soc/Cultural Benefit/Cost	Economic Benefit/Cost	General Comments
Reduce animal numbers	No	Yes	Increases carbon sink because of increasing vegetation cover and better root growth	Reduces animal methane production through reduction in total number	Increases plant cover, increases soil organic matter, and improves productivity	Depends on country and value of animals as a social resource	Depends on the value of livestock products to national and/ or local economy	May require changes in national and/or regional food production policies
Change mix of animals	Yes	Yes	Possible increase in carbon sink with change in plant species	Change to native herbivores reduces emissions in some cases	Potential changes in plant species composition	Depends on country and cultural value of specific animal type	Depends on the value of livestock products	Positive effect in general; improves efficiency of utilization
Alter animal distribution by placing salt licks or feed supplements	Yes	Yes	Increases carbon sink because of increasing vegetation cover overall	Feed supplements may decrease methane production	Useless in rangeland areas already high in salt, but very useful in rangelands low in N,P	Appropriate in countries where animals graze exten- sively, rather than herded	Cost and distribution of salt and supplements	Positive; not applicable for herding systems
Alter animal distribution by placing water resources	Yes	Yes	Potentially increases carbon sink by increasing total vegetation cover	No effect	Developed water resources may not be sustainable	May affect territorial and property boundaries	Motorized water sources often too costly to purchase or maintain	Negative impacts if used to increase numbers of animals
Alter animal distribution by placing fences	No	Yes	Increases carbon sink because of vegetation cover overall	No effect	Benefit is to control domestic animal number and distribution	Depends on country and livestock/ wildlife system	Varies, depending on country and source and kind of materials	Potentially interferes with wildlife migration
Provide livestock protein and phosphorus supplement	Yes	Yes	If supplement increases intake (usual case) and stocking rate is not reduced, soil carbon may decline	Decrease in methane production, especially CH ₄ per unit product	May reduce extensive grazing to some degree	Possible where animals are herded	Cost of protein blocks or similar supplement, but often large increases in productivity	Potentially difficult to distribute to local areas

Table 2-5 continued

Practice	Healthy	Not Healthy	Carbon	Methane	Biophysical Benefit/Cost	Soc./Cultural Benefit/Cost	Economic Benefit/Cost	General Comments
Increase native grasses and/or plant- adapted species	No	Yes	Increases carbon sink because of increasing vegetation cover overall	Possible methane reduction if quality of diet increases, but animals eat more	Benefit in retention of native species for gene conservation	Local people rely on native species for medicine and other health-related goods	Depends on the value of livestock and wildlife products, and the value of herbal medicine	Potential unknown benefits from native species; adapted species survive over the long term
Selective application of herbicides	No	Possibly	Potentially increases carbon sink, although not if woody species removed	Potential increase if animal numbers expand	Cost if non-target species affected: water pollution, damage to food chain	Cost if non-target species affected: water pollution, damage to food chain, removal of firewood source	Varies, depending on country and source of herbicide	Costs or benefits depend on meeting of management goals
Mechanical treatment or restoration	No	Possibly	Potentially increases carbon sink	Potential increase if animal numbers expand	Potential for large-scale alteration of soil and vegetation	May not fit pastoral system	Varies with country, depending on availability of equipment	Benefits depend on success of treatment relative to disruption of ecosystem
Plant halophytes (salt-tolerant species)	If app	ropriate	Increases carbon sink and increases productivity	No known effect	Benefit with increased plant cover and productivity	Benefit with increasing forage production for livestock and wildlife	Cost of planting and maintaining with irrigation	Brings into production otherwise non- productive land
Apply prescribed fire	Yes	Yes	Increases carbon sink and increases productivity in the long term on appropriate rangeland types	by increasing quality of diet	In systems adapted to fire, can increase productivity and maintain nutrient cycling	Use of fire can be part of social system; uses local knowledge	Threat of wildfire and destruction of human resources	Short-term increase in CO ₂ to atmosphere; long-term benefits in adapted systems
Implement agroforestry systems	Yes	Yes	Increases carbon sink and increases productivity in the long term on appropriate rangeland types	Possible methane reduction per unit product by increasing quality of diet	Possible benefit with increased plant cover, diversity, and productivity	Potential benefit with change in grass/browse forage mix for livestock and wildlife	Cost of planting and maintaining	Increases carbon storage in trees; benefit in diversity and productivity if adapted species are used

Table 2-5 continued

Practice	Not Healthy Healthy	Carbon	Methane	Biophysical Benefit/Cost	Soc./Cultural Benefit/Cost	Economic Benefit/Cost	General Comments
Develop large-scale watershed projects	Possibly Possibly	Increases carbon sink and increases productivity	Methane reduction by increasing quality of diet	Potential for large land disturbance, with benefit to human and animal populations because of regulated and regular water supply	Potential for improved food production, both plant and animal	Cost of dams, etc.; benefit of hydroelectric power	Potential for increased human and animal populations because of increase in water availability

food-production systems. However, such projects are expensive and can result in social and cultural dislocation, local extinction of wildlife, and may result in increases in both human and animal population density.

Although rangelands have been used historically for livestock production for meat, wool, hides, milk, blood, and/or pharmaceuticals, policymakers must realize that an equally important objective for maintaining rangelands may be to maximize the number of domestic animals as a social resource (e.g., in some tribal cultures, wives are bought with livestock). Rangelands also are increasingly affected by human activities for mineral production, construction materials, fuel, and chemicals. Additionally, rangelands provide habitat for wildlife, threatened and endangered species, anthropological sites, ecotourism, and recreational activities. As the human population grows, rangelands also incur increased demand for marginal agriculture production. All of these activities and uses potentially affect rangeland condition—and thus the potential of the ecosystem to sequester carbon.

Using the practices in Table 2-5 requires the recognition that productivity on rangelands is variable and that vegetation and animal response to changes in livestock numbers is not linear. Futhermore, there are system lags, and management activities may result in largely irreversible changes in the rangeland system. Risk-management strategies include long-term low stocking or changing animal numbers annually to track variation in precipitation (McKeon *et al.*, 1993). Either approach requires flexible management response to different events, opportunities, and hazards and whole-system analyses in which the interactions of climate, land management, fire, and plant and animal species and communities will determine the outcome.

2.11. Research Needs

We need to know more about the C and N storage capacity of soils under different conditions of degradation and under different land uses and land management, as well as the potential for increased sequestration of C, especially in whole-system analyses. More information is needed regarding the actual release rates of various greenhouse gases in real environments, across the spectrum of climates, soils, and land uses (rather than the current measurements just from a few points) and land management. Our lack of ability to track plant responses within growing season also affects our ability to accurately estimate rapid changes in greenhouse gas fluxes and remains a major gap in our ability to link management practices with global climate-change issues.

Rangeland research on climate-change effects should emphasize multispecies field experiments. The concept of functional groups might be a way to cope with the overwhelming species diversity of most rangelands, especially grasslands. Models that incorporate nonequilibrium theory in grassland and rangeland ecosystem response would be most useful.

Rangeland research emphasis should be on multidisciplinary projects in which different components (e.g., vegetation, soil, herbivores) and various approaches (e.g., conservation, economic sustainability) are simultaneously considered. Maintenance of long-term monitoring sites is essential for understanding boundary changes (especially C_3/C_4 , shrub/grass boundaries), as well as fire, herbivory, and land-use affects on rangeland productivity and diversity. Along with monitoring, there needs to be an ongoing analysis of the results and review of monitoring methods and criteria.

Information on various aspects of climate, community structure and function, and land use needs to be standardized.

At a national level, scientists and policymakers must better understand the implications of land use for global-change issues, because land use and management feeds into global change as well as being influenced by it. The interaction between human population growth and rangeland use must also be better understood. Land use will change in the future as a result of altered climatic extremes (especially those in rainfall and temperature), decreased productivity and soil fertility,

and possibly socioeconomic changes spurred by adaptation and mitigation requirements.

Interfacing research on global change effects on agroecosystems with those on rangeland systems would be helpful in that it would promote access to a greater range of databases and models. The International Geosphere Biosphere Programme (IGBP)—Global Change and Terrestrial Ecosystems (GCTE) Project Task 3.1.3 (Pastures and Rangelands) (Campbell and Stafford Smith, 1993; Stafford Smith *et al.*, 1995) is combining the research efforts of grassland scientists in improved pastures and rangeland systems to predict global-change effects on the whole spectrum of different grassland types, taking into account future land-use change.

Finally, detailed analyses of the potential biological effects of climate change in terms of rangeland boundaries, coupled with an economic assessment of potential effects on pastoral peoples and national economies, will improve future assessments of impact, adaptation, and mitigation potentials on rangelands.

References

- Abrams, M.E., A.K. Knapp, and L.C. Hulbert, 1986: A ten-year record of aboveground biomass in Kansas tallgrass prairie: effects of fire and topographic position. *American Journal of Botany*, 73, 1506-1515.
- Aceituno, P., 1988: On the functioning of the Southern-Oscillation in the South America sector. Part I: Surface climate. Mon. Wea. Rev., 116, 505-524.
- Ågren, G.I., R.E. McMurtrie, W.J. Parton, J. Pastor, and H.H. Shugart, 1991: State-of-the-art of models of production decomposition linkages in conifer and grassland ecosystems. *Ecological Applications*, 1, 118-138.
- Alcamo, J. (ed.), 1994: IMAGE 2.0: Integrated Modeling of Global Climate Change. Kluwer Academic Publishers, Dordrecht, Netherlands, 318 pp.
- Allen, Jr., L.H., E.C. Bisbal, K.J. Boote, and P.H. Jones, 1991: Soybean dry matter allocation under subambient and superambient levels of carbon dioxide. Agronomy Journal, 83, 875-883.
- Anderson, I.C., J.S. Levine, M.A. Poth, and P.J. Riggan, 1988: Enhanced biogenic emissions of nitric oxide and nitrous oxide following surface biomass burning. *Journal of Geophysical Research*, 93, 3893-3898.
- Anderson, J.M., 1991: The effects of climate change on decomposition processes in grassland and coniferous forests. *Ecological Applications*, 1(3), 326-247.
- Arana, S.C., N.H. Mailland, S.I. Alonso, N.O. Maceira, and C.A. Verona, 1985: Crecimiento y fenologia de poblaciones vegetales en un pastizal natural. Su significado adaptativo. RIA (INTA), 20, 105-134.
- Archer, S., 1994: Woody plant encroachment into Southwestern grasslands and savannas: rates, patterns and proximate causes. In: Ecological Implications of Livestock Herbivory in the West [Vavra, M., W.A. Laycock, and R.D. Pieper (eds.)]. Society for Range Management, Denver, CO, pp. 13-68.
- Archer, S., D.S. Schimel, and E.A. Holland, 1995: Mechanisms of shrubland expansion: land use, climate or CO,? *Climate Change*, **29**, 91-100.
- Archer, S. and F.E. Smeins, 1991: Ecosystem-level processes. In: Grazing Management: An Ecological Perspective [Heitschmidt, R.K. and J.W. Stuth (eds.)]. Timberline Press, Portland, OR, pp. 109-139.
- Arhem, K., 1985: Pastoral Man in the Garden of Eden. University of Uppsala, Uppsala, Sweden, 123 pp.
- Ash, A.J., S.M. Howden, and J.G. McIvor, 1995: Improved rangeland management and its implications for carbon sequestration. Proc. Vth International Rangelands Congress, Salt Lake City, Utah (in press).
- Ayres, M.P., 1993: Plant defense, herbivory, and climate change. In: Biotic Interactions and Global Change [Karelva, P.M., J.G. Kingsolver, and R.B. Huey (eds.)]. Sinauer Assoc. Inc., Sunderland, MA, pp. 75-94.

- Bailey, R.G., 1986: A world ecoregions map for resource reporting. *Environmental Conservation*, **13**(3), 195-202.
- Bailey, R.G., 1989: Explanatory supplement to ecoregions map of the continents. *Environmental Conservation*, **16(4)**, 307-310.
- Baker, J.T., L.H. Allen, Jr., and K.J. Boote, 1990: Growth and yield responses of rice to carbon dioxide concentration. *Journal of Agricultural Science*, 115, 313-320.
- Barbour, J.G., J.H. Burk, and W.D. Pitts (eds.), 1987: Terrestrial Plant Ecology. The Benjamin/Cummings Publishing Company, Inc., Menlo Park, CA, 634 pp.
- Bauer, A. and A.L. Black, 1981: Soil carbon, nitrogen and bulk density comparisons in two crop land tillage systems after 25 years and in virgin grassland. Soil Science Society of America Journal, 45, 1166-1170.
- Bazzaz, F.A. and K.D.M. McConnaughay, 1992: Plant-plant interactions in elevated CO₂ environments. *Australian Journal of Botany*, **40**, 547-563.
- Bazzaz, F.A. and E.D. Fajer, 1992: Plant life in a CO₂-rich world. Scientific American, 266, 68-74.
- Bazzaz, F.A., 1993: Scaling in biological systems: population and community perspectives. In: Scaling Physiological Processes: Leaf to Globe [Ehleringer, J.R. and C.B. Field (eds.)]. Academic Press, Inc., San Diego, pp. 159-166.
- Bazzaz, F.A., 1990: The response of natural ecosystems to the rising global CO₂ levels. *Annual Review of Ecological Systems*, **21**, 167-196.
- Behnke, R., I. Scoones, and C. Keerven (eds.), 1993: Range Ecology at Disequilibrium. Overseas Development Institute, London, UK, 248 pp.
- **Bekure**, S., P.N. de Leeuw, and B.E. Grandin, 1987: *Maasai Herding. An Investigation of Pastoral Production on Group Ranches in Kenya*. International Livestock Center for Africa, Nairobi, Kenya, 158 pp.
- **Berdowski**, J.J.M., 1987: Transition from heathland to grassland initiated by the heather beetle. *Vegetatio*, **72**, 167-173.
- Biederbeck, V.O., C.A. Campbell, K.E. Bowren, M. Schnitzer, and R.N. McIver, 1980: Effect of burning on cereal straw, on soil properties and grain yields in Saskatchewan. Soil Science Society of America Journal, 44, 103-111.
- **Billings**, W.D., K.M. Peterson, J.O. Luken, and D.A. Mortensen, 1984: Interaction of increasing atom carbon dioxide and soil nitrogen on the carbon balance tundra microcosms. *Oecologia*, **65**, 26-29.
- Bisset, W.J., 1962: The black speargrass (heteropogon contortus) problem of the sheep country in central western Queensland. *Queensland Journal of Agricultural Sciences*, 19, 189-207.
- Bonan, G.B., D. Pollard, and S.L. Thompson, 1992: Effects of boreal forest vegetation on global climate. *Nature*, **359**(**6397**), 716-718.
- **Bouwman**, A.F., 1993: Inventory of greenhouse gas emissions in the Netherlands. *Ambio*, **22**, 519-523.
- **Bouwman**, A.F., 1994: Computing land use emissions of greenhouse gases. *Water, Air, and Soil Pollution*, **76**, 231-258.
- **Bouwman**, A.F., K.W. Van der Hoek, and J.G.J. Olivier, 1995: Uncertainties in the global source distribution of nitrous oxide. *JGR-Atmospheres*, **100**, 2785-2800.
- **Briske**, D.D. and R.K. Heitschmidt, 1991: An ecological perspective. In: *Grazing Management: An Ecological Perspective* [Heitschmidt, R.K. and J.W. Stuth (eds.)]. Timber Press Inc., Portland, OR, pp. 11-27.
- Brown, J., 1994: Antarctic ozone going fast but some plants can survive. New Scientist, 143, 11.
- Buol, S.W., P.A. Sanchez, S.B. Weed, and J.M. Kimble, 1990: Predicted impact of climatic warming on soil properties and use. In: *Impact of Carbon Dioxide, Trace Gases, and Climate Change on Global Agriculture* [Kimball, B.A., N.J. Rosernberg, and L.H. Allen, Jr. (eds.)]. ASA Special Publ. No. 53, American Society of Agronomy, Crop Science Society of America, and Soil Science Society of America, Madison, WI, pp. 71-82.
- Burke, I.C., C.M. Yonker, W.J. Parton, C.V. Cole, K. Flach, and D.S. Schimel, 1989: Texture, climate and cultivation effects on soil organic matter content in U.S. grassland soils. Soil Science Society of America Journal, 53, 800-805.
- Burke, I.C., T.G.F. Kittel, W.K. Lauenroth, P. Snook, C.M. Yonker, and W.J. Parton, 1990. Regional analysis of the Central Great Plains: sensitivity to climate variability. *Bioscience*, 41, 685-692.

- Burke, I.C., W.K. Lauenroth, and D.P. Coffin, 1995a: Recovery of soil organic matter and N mineralization in semiarid grasslands: implications for the Conservation Reserve Program. *Ecological Applications* (in press).
- Burke, I.C., E.T. Elliott, and C.V. Cole, 1995b: Influence of macroclimate and landscape position and management on nutrient conservation and nutrient supply in agroecoystems. *Ecological Applications*, 5, 124-131.
- Cabrera, A.L., 1976: Regiones Fitogeográficas Argentinas. ACME, Buenos Aires, Argentina.
- Caceres, D.M., 1993: Peasant Strategies and Models of Technological Change: A Case Study from Central Argentina. M.Phil. thesis, University of Manchester, Manchester, UK.
- Caldwell, M.M., A.H. Termaura, and M. Tevini, 1989: The changing solar ultraviolet climate and the ecological consequences for higher plants. *Trends in Ecology and Evolution*, 4, 363-367.
- Campbell, D.J., 1984: Response to drought among farmers and herders in southern Kajiado District, Kenya. Human Ecology, 12(1), 35-64.
- Campbell, B.D. and J.P. Grime, 1993: Prediction of grassland plant responses to global change. In: *Proceedings of the XVII International Grassland Congress*. pp. 1109-1118.
- Campbell, B.D. and R.M. Hay, 1993: Will subtropical grasses continue to spread through New Zealand? In: *Proceedings of the XVII International Grassland Congress*. pp. 1126-1128.
- Campbell, B.D. and M. Stafford Smith, 1993: Defining GCTE modelling needs for pastures and rangelands. In: Proceedings of the XVII International Grassland Congress. pp. 1249-1253.
- Campbell, B.D., G.M. McKeon, R.M. Gifford, H. Clark, M.S. Stafford Smith, P.C.D. Newton, and J.L. Lutze, 1995a: Impacts of atmospheric composition and climate change on temperate and tropical pastoral agriculture. In: *Greenhouse '94* [Pearman, G.I. and M.R. Manning (ed.)]. CSIRO, Melbourne, Australia (in press).
- Campbell, B.D., W.A. Laing, D.H. Greer, J.R. Crush, H. Clark, D.Y. Williamson, and M.D.J. Given, 1995b: Prediction of adaptive changes in improved temperate pastures as a result of global change. *Journal of Biogeography* (in press).
- Carras, J.N., P.J. Fraser, D.W.T. Griffith, D.F. Hurst, and D.J. Williams, 1994: Trace gas emissions from Australian savannah fires during the 1990 dry season. *Journal Atmospheric Chemistry*, 18(1), 33-56.
- Chaneton, E.J., J.M. Facelli, and R.J.C. León, 1988: Floristic changes induced by flooding on grazed and ungrazed lowland grasslands in Argentina. *Journal of Range Management*, 41, 495-499.
- Chapin, F.S. III and G.R. Shaver, 1985: Individualistic growth response of tundra plant species to environmental manipulations in the field. *Ecology*, 66, 564-576.
- Chapin, F.S. III, G.R. Shaver, A.E. Giblin, K.G. Nadelhoffer, and J.A. Laundre, 1995: Response of arctic tundra to experimental and observed changes in climate. *Ecology*, 76, 694-711.
- Cherfas, J., 1992: Cloudy issues, burning answers. The Independent, 9/7.
- Cicerone, R.J. and R. Oremland, 1988: Biogeochemical aspects of atmospheric methane. Global Biogeochemical Cycles, 2, 299-327.
- Coffin, D.P. and W.K. Lauenroth, 1990: A gap dynamics simulation model of succession in a semiarid grassland. Ecol. Modelling, 49, 229-266.
- Cole, C.V., I.C. Burke, W.J. Parton, D.S. Schimel, D.S. Ojima, and J.W.B. Stewart, 1990: Analysis of historical changes in soil fertility and organic matter levels of the North American Great Plains. In: *Challenges in Dryland Agriculture*. A Global Perspective [Unger, P.W., T.V. Sneed, W.R. Jordon, and R. Jensen (eds.)]. Proceedings of the International Conference on Dryland Farming, August 1988, Austin, TX, pp 436-438.
- Cole, C.V., J.W.B. Stewart, D.S. Ojima, W.J. Parton, and D.S. Schimel, 1989: Modeling land use effects on soil organic matter dynamics in the North American Great Plains. In: *Ecology of Arable Land—Perspectives and Challenges. Developments in Plant and Soil Sciences* [Clarholm, M. and L. Bergstrom (eds.)] Kluwer Academic Publishers, Dordrecht, Netherlands, 39, pp. 89-98.
- Coleman, J.S., K.D.M. McConnaughay, and F.A. Bazzaz, 1993: Elevated CO₂ and plant nitrogen use: is reduced tissue nitrogen concentration size-dependent? *Oecologia*, 93, 195-200.
- Comins, H.N. and R.E. McMurtrie, 1993: Long-term response of nutrient limited forests to CO₂ enrichment: equilibrium behavior of plant-soil models. *Ecological Applications*, 3, 666-681.

- Conroy, J.P., 1992: Influence of elevated atmospheric CO₂ concentrations on plant nutrition. *Australian Journal of Botany*, **40**, 445-456.
- Coughenour, M.B., 1984: A mechanistic simulation analysis of water use, leaf angles, and grazing in East African graminoids. *Ecological Modelling*, 26, 203-220.
- Coughenour, M.B., J.E. Ellis, D.M. Swift, D.L. Coppock, K. Galvin, J.T. McCable, and T.C. Hart, 1985: Energy extraction and use in a nomadic pastoral ecosystem. *Science*, 230(4726), 619-625.
- Coutinho, L.M., 1982: Ecological effects of fire in Brazilian cerrado. In: Ecology of Tropical Savannas [Huntley, B.J. and B.H. Walker (eds.)]. Springer-Verlag, Berlin, Germany, pp. 273-291.
- Crush, J.R., B.D. Campbell, and J.P.M. Evans, 1993: Effect of elevated atmospheric CO₂ levels on nodule relative efficiency in white clover. In: *Proceedings of the XVII International Grassland Congress*. pp. 1131-1133.
- Crutzen, P.J. and M.O. Andreae, 1990: Biomass burning in the tropics: impact on atmospheric chemistry and biogeochemical cycles. *Science*, 250, 1669-1678.
- D'Antonio, C.M. and P.M. Vitousek, 1992: Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annual Review of Ecological Systems*, 23, 63-87.
- Dacey, J.W.H., B.G. Drake, and M.J. Klug, 1994: Stimulation of methane emission by CO₂ enrichment of marsh vegetation. *Nature*, **370**, 47.
- Daubenmire, R., 1968: Ecology of fire in grasslands. *Advanced Ecological Research*, **5**, 209-266.
- Davidson, E.A., 1991: Fluxes of nitrous oxide and nitric oxide from terrestrial ecosystems. In: Microbial Production and Consumption of Greenhouse Gases: Methane, Nitrogen Oxides, and Halomethanes [Rogers, J.A. and W.B. Whitman (eds.)]. American Society for Microbiology, Washington DC.
- **Dentener**, F.J. and P.J. Crutzen, 1994: A three dimensional model of the global ammonia cycle. *Journal of Atmospheric Chemistry*, **19**, 331-369.
- Deregibus, V.A., 1988: Importancia de los pastizales naturales en la República Argentina: situación present y future. Revista Argentina de Producción Animal, 8, 67-78.
- de Ridder, N., L. Stroosnijder, A.M. Cisse, and H. van Keulen, 1982: PPS course book. Vol. I, Theory. In: Productivity of Sahelian Rangelands: A Study of the Soils, the Vegetations and the Exploitation of That Natural Resource. Wageningen Agricultural University, Department of Soil Science and Plant Nutrition, Wageningen, Netherlands, pp. 227-231.
- Diaz, S., 1995: Elevated CO_2 responsiveness, interactions at the community level, and plant functional types. *J. Biogeography*, 22 (in press).
- Díaz, S., J.P. Grime, J. Harris, and E. McPherson, 1993: Evidence of a feed-back mechanism limiting plant response to elevated carbon dioxide. Nature, 364, 616-617.
- **Dickinson**, R.E. and A. Henderson-Sellers, 1988: Modeling tropical deforestation: a study of GCM land-surface parameterizations. *Q. J. R. Meteorol. Soc.*, **114**, 439-462.
- Dyer, M.I., C.L. Turner, and T.R. Seastedt, 1993: Herbivory and its consequences. *Ecological Applications*, 3, 10-16.
- Easterling, W.E., 1990: Climate trends and prospects. In: *Natural Resources for the 21st Century* [Sampson, R.N. and D. Hair (eds.)]. Island Press, Washington DC, pp. 32-55.
- Ehleringer, J.R. and C.B. Field (eds.), 1993: Scaling Physiological Processes: Leaf to Globe. Academic Press, New York, NY, 388 pp.
- Ellis, J. and K.A. Galvin, 1994: Climate patterns and land use practices in the dry zones of east and west Africa. *Bioscience*, 44(5), 340-349.
- Ellis, J.E., K.A. Galvin, J.T. McCabe, and D.M. Swift, 1990: *Pastoralism and Drought in Turkana District, Kenya*. A Report to NORAD, Development Systems Consultants, Inc., Bellvue, CO.
- Ellis, J. and D.M. Swift, 1988: Stability of African pastoral ecosystems: alternate paradigms and implications for development. *Journal of Range Management*, **41**, 450-459.
- Emanuel, W.R., H.H. Shugart, and M.P. Stevenson, 1985: Climatic change and the broad-scale distribution of terrestrial ecosystems. Climate Change, 7, 29-43.
- Evans, P.A. and M.R. Ashmore, 1992: The effects of ambient air on a seminatural grassland community. Agric. Ecosyst. Environ., 38(1-2), 91-97.
- Evans, E.W. and T.R. Seastedt, in press: The relations of phytophagous invertebrates and rangeland plants. In: Rangeland Plant Morphology and Physiology [Bedunah, D.J. (ed.)]. Society for Range Management, Denver, CO.

- Fajer, E.D., M.D. Bowers, and F.A. Bazzaz, 1989: The effects of enriched carbon dioxide atmospheres on plant-insects herbivore interactions. *Science*, 243, 1198-1200.
- Fajer, E.D., M.D. Bowers, and F.A. Bazzaz, 1991: The effects of enriched CO₂ atmospheres on the buckeye butterfly, Junonia coenia. *Ecology*, 72, 751-754.
- Farinas, M. and J.J. San José, 1987. Cambios en el estrato herbáceo de una parcela de sabana protegida del fueo y del pastoreo durante 23 años. Calabozo. Venezuela. Acta Científica Venezolana, 36, 199-200.
- Fernández-A, R.J., O.E. Sala, and R.A. Golluscio, 1991: Woody and herbaceous aboveground production of a Patagonian steppe. *Journal of Range Management*, 44, 434-437.
- Firestone, M.K. and E.A. Davidson, 1989: Microbial basis of NO and N₂O production and consumption in soil. In: Exchange of Trace Gases Between Terrestrial Ecosystems and the Atmosphere [Andreae, M.O. and D. Schimel (eds.)]. John Wiley and Sons, Chichester, UK.
- Fisher, M.J., I.M. Rao, M.A. Ayarza, C.E. Lascano, J.I. Sanz, R.J. Thomas, and R.R. Vera, 1994: Carbon storage by introduced deep-rooted grasses in the South American savannas. *Nature*, 371, 236-238.
- Foran, B.D., G. Bastin, E. Remenga, K.W. Hyde, 1982: The response to season, exclosure and distance from water of three central Australian pasture types grazed by cattle. *Australian Rangeland Journal*, 4, 5-15.
- Frost, P., E. Medina, J.C. Menaut, O. Solbrig, M.J. Swift, and B. Walker (eds.), 1986: Responses of savannas to stress and disturbance: a proposal for a collaborative program of research. In: *Biology International*, Special Issue No. 10. International Union of Biological Sciences, Paris, France, pp. 1-82.
- Galvin, K.A., 1992: Nutritional ecology of pastoralists in dry tropical Africa. American Journal of Human Biology, 4(2), 209-221.
- Galvin, K.A., D.L. Coppock, and P.W. Leslie, 1994: Diet, nutrition and the pastoral strategy. In: African Pastoralist Systems: An Integrated Approach [Fratkin, E., K.A. Galvin, and E.A. Roth (eds.)]. Lynne Rienner, Boulder, CO, pp. 113-132.
- Gifford, R.M., 1977: Growth pattern, carbon dioxide exchange and dry weight distribution in wheat growing under differing photosynthetic environments. Australian Journal of Plant Physiology, 4, 99-110.
- Gifford, R.M., 1994: The global carbon cycle: a viewpoint about the missing carbon. Australian Journal of Plant Physiology, 21, 1-15.
- Goldstein, G. and G. Sarmiento, 1987: Water relations of trees and grasses and their consequences for the structure of savanna vegetation. In: *Determinants of Tropical Savannas*. IUBS Monograph Series 3, IRL Press Ltd, Oxford, UK, pp. 13-38.
- Graetz, R.D., B.H. Walker, and P.A. Walker, 1988: The consequences of climatic change for seventy percent of Australia. In: Greenhouse. Planning for Climate Change. CSIRO, Division of Atmospheric Research, Melbourne, Australia, pp. 399-420.
- Greco, S., R.H. Moss, D. Viner, and R. Jenne, 1994: Climate Scenarios and Socioeconomic Projections for IPCC WGII Assessment. IPCC-WMO and UNEP, Washington DC, 67 pp.
- Griffin, G.F. and M.H. Friedel, 1985: Discontinuous change in central Australia: some implications of major ecological events for land management. *Journal of Arid Environments*, 9, 63-80.
- Grulke, N.E., G.H. Riechers, W.C. Oechel, U. Hjelm, and C. Jaeger, 1990: Carbon balance in tussock tundra under ambient and elevated CO₂. *Oecologia*, 83, 485-494.
- Haas, H.J., C.E. Evans, and E.F. Miles, 1957: Nitrogen and Carbon Changes in Great Plains Soils Influenced by Cropping and Soil Treatments. Technical Bulletin 1164, USDA, Washington DC, 111 pp.
- Hall, D.O. and J. Scurlock, 1991: Tropical grasslands and their role in the global carbon cycle. In: *Facets of Modern Ecology* [Esser, G. and D. Overdick (eds.)]. Elsevier, Amsterdam, Netherlands, pp. 555-573.
- Hanson, J.D., B.B. Baker, and R.M. Bourdon, 1993: Comparison of the effects of different climate change scenarios on rangeland livestock production. *Agricultural Systems*, 41(4), 487-502.
- **Hastings**, J.R. and R.M. Turner, 1965: *The Changing Mile*. University of Arizona Press, Tucson, AR, 317 pp.
- Havstrom, M., T.V. Callaghan, and S. Jonasson, 1993: Differential growth responses of Cassiope tetragona, an arctic dwarf-shrub, to environmental perturbations among three contrasting high- and sub-arctic sites. *Oikos*, 66, 389-402.

- Heady, H.F. (ed.), 1988: The Vale Rangeland Rehabilitation Program: An Evaluation. Resource Bulletin PNW-RB-157, USDI Bureau of Land Management, USDA Forest Service, Portland, OR, 151 pp.
- **Heady**, H.F. and R.D. Childs, 1994: *Rangeland Ecology and Management*. Westview Press, Boulder, CO, 519 pp.
- **Heitschmidt**, R.K. and J.W. Stuth, 1991: *Grazing Management*. *An Ecological Perspective*. Timber Press, Portland, OR, 259 pp.
- **Henderson-Sellers**, A. and K. McGuffie, 1995: Global climate models and 'dynamic' vegetation changes. *Global Change Biology*, **1**, 63-75.
- Hicks, R.A., D.D. Briske, C.A. Call, and R.J. Ansley. 1990: Co-existence of a perennial C₃ bunchgrass in a C₄ dominated grassland: an evaluation of gas exchange characteristics. *Photosynthetica*, 24, 63-74.
- **Hobbs**, R.J. and L.F. Huenneke, 1992: Disturbance, diversity and invasion: implication for conservation. *Conservation Biology*, **6**, 324-337.
- **Hobbs**, R.J., D.S. Schimel, C.E. Owensby, and D.S. Ojima, 1991: Fire and grazing in the tallgrass prairie: contingent effects on nitrogen budgets. *Ecology*, **72**, 1374-1382.
- Holdridge, L.R., 1947: Determination of world plant formations from simple climate data. Science, 105, 367-368.
- Holland, E.A. and J.K. Detling, 1990: Plant response to herbivory and below ground nitrogen cycling. *Ecology*, 71, 1040-1049.
- Holland, E.A., W.J. Parton, J.K. Detling, and D.L. Coppock, 1992: Physiological responses of plant populations to herbivory and their consequences for ecosystem nutrient flow. *American Naturalist*, 142, 685-706.
- **Homewood**, K.M. and W.A. Rodgers, 1984: Pastoralism and conservation. *Human Ecology*, **12**, 431-442.
- Homewood, K., W.A. Rodgers, and K. Arhem, 1987: Ecology of pastoralism in Ngorongoro Conservation Area, Tanzania. *Journal of Agricultural Science, Cambridge*, 108, 47-72.
- Howden, S.M., 1991: Methane production from livestock. Draft Australian Greenhouse Gas Emissions Inventory 1987-88. Greenhouse Studies, 10 (DASET), 15-22.
- **Howden**, S.M., D.H. White, G.M. McKeon, J.C. Scanlan, and J.O. Carter, 1994: Methods for exploring management options to reduce greenhouse gas emissions from tropical pastures. *Climate Change*, **30**, 49-70.
- Hulbert, L.C., 1988: Causes of fire effects in tallgrass prairie. Ecology, 69, 46-58
- Hulme, M., 1990: The changing rainfall resources of Sudan. *Transactions*, *Institute of British Geographers*, **15**, 21-34.
- Hunt, H.W., M.J. Trlica, E.F. Redente, J.C. Moore, J.K. Detling, T.G.F. Kittel, D.E. Walter, M.C. Fowler, D.A. Klein, and E.T. Elliott, 1991: Simulation model for the effects of climate change on temperate grassland ecosystems. *Ecological Modelling*, 53, 205-246.
- **Hutsch**, B.W., C.P. Webster, and D.S. Powlson, 1995: Methane oxidation in soil as affected by land use, soil pH and N fertilization. *Soil Biology and Biochemistry*, **24**, 1613-1622.
- Idso, K.E. and S.B. Idso, 1994: Plant responses to atmospheric CO₂ enrichment in the face of environmental constraints: a review of the last 10 years' research. *Aric. For. Meteorol.*, 69, 153-203.
- Idso, S.B. 1989: Carbon Dioxide and Global Change: Earth in Transition. IBR Press, Tempe, AR, 292 pp.
- IPCC, 1990: Climate Change: The IPCC Scientific Assessment [Houghton, J.T., G.J. Jenkins, and J.J. Ephraums (eds.)]. Cambridge University Press, Cambridge, UK, 365 pp.
- IPCC, 1992: Climate Change 1992. The Supplementary Report to the IPCC Scientific Assessment [Houghton, J.T., B.A. Callander, and S.K. Varney (eds.)]. Cambridge University Press, Cambridge, UK, 200 pp.
- Jenkinson, D.S., 1977: Studies on the decomposition of plant material in soil.
 V. The effects of plant cover and soil type on the loss of carbon from ¹⁴C labeled rye grass decomposing under field conditions. *Journal of Soil Science Society of America*, 28, 424-494.
- Jenkinson, D.S., J.M. Potts, J.N. Perry, V. Burnett, K. Coleman, and A.E. Johnston, 1994: Trends in herbage yields over the last century on the Rothamsted Long-Term Continuous Hay experiment. *Journal of Agricultural Science, Cambridge*, 122, 365-374.
- **Johnson**, R.H. and D.E. Lincoln, 1991: Carbon allocation patterns and grasshopper nutrition—the influence of CO₂ enrichment and soil mineral limitation. *Oecologia*, **87**, 127-134.

- Keller, M., E. Veldkamp, A. Weitz, and W. Reiners, 1993: Effect of pasture age on soil trace gas emissions from a deforested area of Costa Rica. *Nature*, 365, 244-246.
- Kemp, P.R. and G.J. Williams III, 1980: A physiological basis for niche separation between Aropyron smithii (C₃) and Bouteloua racilis (C₄). Ecology, 61, 846-858.
- Kielland, K., 1990: Processes Controlling Nitrogen Release and Turnover in Arctic Tundra. Ph.D. diss., University of Alaska, Fairbanks, AK.
- Kimball, B.A., 1983: Carbon dioxide and agricultural yield: an assemblage and analysis of 430 prior observations. Agronomy Journal, 75, 779-788.
- Kimball, B.A., J.R. Mauney, F.S. Nakayama, and S.B. Idso, 1993: Effects of elevated CO₂ and climate variables on plants. *Journal Soil Water Conservation*, 48, 9-14.
- Kimball, B.A., N.J. Rosenberg, and L.H. Allen, Jr. (eds.), 1990: Impact of Carbon Dioxide, Trace Gases, and Climate Change on Global Agriculture. ASA Spec. Publ. No. 53, American Society of Agronomy, Crop Science Society of America, and Soil Science Society of America, Madison, WI, 133 pp.
- King, G.M. and S. Schnell, 1994: Effect of increasing atmospheric methane concentration on ammonium inhibition of soil methane consumption. *Nature*, 370, 282-284.
- Knapp, A.K., 1984: Post-burn differences in solar radiation, leaf temperature and water stress influencing production in lowland tallgrass prairie. *American Journal of Botany*, 71, 220-227.
- Knapp, A.K., 1985: Effect of fire and drought on ecophysiology of Andropogon gerardii and Panicum virgatum in tallgrass prairie. *Ecology*, 66, 1309-1320.
- Knapp, A.K. and T.R. Seastedt, 1986: Detritus accumulation limits the productivity of tallgrass prairie. *Bioscience*, 36, 662-668.
- Koizumi, H., T. Nakadai, Y. Usami, M. Satoh, M. Shiyomi, and T. Oikawa, 1991: Effect of carbon dioxide concentration on microbial respiration in soil. *Ecol. Res.*, 6, 227-232.
- Korner, C., 1993: CO₂ fertilization: the great uncertainty in future vegetation development. In: *Vegetation Dynamics and Global Change* [Solomon, A.M. and H.H. Shugart (eds.)]. Chapman & Hall, New York, NY, pp. 53-70.
- Korner, C. and F. Miglietta, 1994: Long term effects of naturally elevated CO₂ on mediterranean grassland and forest trees. *Oecologia*, 99, 343-351.
- Krupa, S.V. and R.N. Kickert, 1989: The greenhouse effect: impacts of ultraviolet-B (UV-B) radiation, carbon dioxide (CO₂) and ozone (O₃) on vegetation. *Environmental Pollution*, 61, 263-393.
- Kucera, C.L., 1981: Grasslands and fire. In: Fire Regimes and Ecosystem Properties. U.S. Forest Gen. Tech. Rep. WO-26, USDA, Washington DC, 594 pp.
- **Lauenroth**, W.K. and O.E. Sala, 1992: Long-term forage production of North American shortgrass steppe. *Ecological Applications*, **2**, 397-403.
- Lavrenko, E.M. and Z.V. Karamysheva, 1992: Steppes of the former Soviet Union and Mongolia. In: *Natural Grassland*. Elsevier, Amsterdam and New York, pp. 3-59.
- Lean, G., D. Hinrichsen, and A. Markham, 1990: Atlas of the Environment. Prentice Hall Press, New York, NY, 192 pp.
- Le Houerou, H.N., 1984: Rain use efficiency: a unifying concept in arid-land ecology. *Journal of Arid Environments*, 7, 213-247.
- Le Houerou, H.N. and C.H. Hoste, 1977: Rangeland production and annual rainfall relations in the Mediterranean basin and in the African Shelo-Sudanian zone. *Journal of Range Management*, 30, 181-189.
- Lewis, J.P., E.F. Pire, D.E. Prado, S.L. Stofella, E.A. Franceschi, and N.J. Carnevali, 1990: Plant communities and phytogeographical position of a large depression in the Great Chaco, Argentina. *Vegetatio*, **86**, 25-38.
- Little, P.D., 1987: Land use conflicts in the agricultural/pastoral borderlands: the case of Kenya. In: Lands at Risk in the Third World [Little, P.D., M.M. Horowitz, and A.E. Nyerges (eds.)]. Westview, Boulder, CO, pp. 195-212.
- Lodman, D.W., M.E. Branine, B.R. Carmen, P. Zimmerman, G.M. Ward, and D.E. Johnson, 1993: Estimates of methane emissions from manure of United States cattle. *Chemosphere*, 26, 189-200.
- Long, S.P. and P. Hutching, 1991: Primary production in grasslands and coniferous forests with climate change: an overview. *Ecological Applications*, 1, 139-156.
- Londsdale, M. and R. Braithwaite, 1988: The shrub that conquered the bush. New Scientist, 15, 52-55.

- Mann, G.F., 1966: Bases Ecológicas de la Explotación Agropacuaria en América Latina. OEA, Chile.
- Marion, G.M., D.S. Introve, and K. Vaneleve, 1991: The stable isotope geochemistry of CaCO₃ on the Tanana River floodplain of interior Alaska, USA—Composition and mechanisms of formation. *Chemical Geology*, 86, 97-110.
- Maxwell, B., 1992: Arctic climate: potential for change under global warming. In: Arctic Ecosystems in a Changing Climate: An Ecosphysiological Perspective [Chapin, F.S. III, R.L. Jeffereies, J.F. Reynolds, G.R. Shaver, and J. Svoboda (eds.)]. Academic Press, San Diego, CA, pp. 11-34.
- Mayeux, H.S., H.B. Johnson, and H.W. Polley, 1991: Global change and vegetation dynamics. In: *Noxious Range Weeds* [James, L.F., J.O. Evans, M.H. Ralphs, and R.D. Child (eds.)]. Westview Press, Boulder, CO, pp. 62-74.
- McCabe, J.T., 1990: Turkana pastoralism. A case against the tragedy of the commons. *Human Ecology*, 18, 81-104.
- McGuire, A.D., J.M. Melillo, L.A. Joyce, D.W. Kicklighter, A.L. Grace, B. Moore III, and C.J. Vorosmarty, 1992: Interactions between carbon and nitrogen dynamics in estimating net primary productivity for potential vegetation in North America. Global Biogeochemical Cycles, 6, 101-124.
- McKeon, G.M., S.M. Howden, et al., 1989: The effect of climate change on crop and pastoral production in Queensland. In: *Greenhouse: Planning for Climate Change*. CSIRO, Melbourne, Australia, pp. 546-565.
- McKeon, G.M., K.A. Day, S.M. Howden, J.J. Mott, D.M. Orr, W.J. Scattini, and E.J. Weston, 1990: Northern Australian savannas: management for pastoral production. *Journal of Biogeography*, 17, 355-372.
- McKeon, G.M. and S.M. Howden, 1991: Adapting northern Australian grazing systems to climatic change. *Climate Change Newsletter*, **3**(1), 5-8.
- McKeon, G.M., S.M. Howden, N.O.J. Abel, and J.M. King, 1993: Climate change: adapting tropical and sub-tropical grasslands. In: Proc. of the XVIIth International Grassland Congress, Palmerston North, New Zealand. pp. 1181-1190.
- **Medina**, E., 1982: Physiological ecology of neotropical savanna plants. In: *Ecology of Tropical Savannas* [Hyntley, B.J. and B.H. Walker (eds.)]. Springer-Verlag, Berlin, Germany, pp. 308-335.
- Medina, E., 1986: Forests, savannas and monyane tropical environments. In: Photosynthesis in Contrasting Environments [Baker, N.R. and S.P. Long (eds.)]. Elsevier Science Publishers, B.V., Amsterdam and New York, pp. 139-171.
- Medina, E., 1987: Nutrients, requirements, conservation and cycles in the herbaceous layer. In: *Determinants of Tropical Savannas*. IVBS Monograph Series No. 3, IRL Press LTD, Oxford, UK, pp. 39-65.
- **Medina**, E. and J. Silva, 1990: Savannas of the northern South America: a steady state regulated by water-fire interactions on a background of low nutrient availability. *Journal of Biogeography*, **17**, 403-413.
- Milchunas, D.G., O.E. Sala, and W.K. Lauenroth, 1988: A generalized model of the effects of grazing by large hervibores on grassland community structure. *American Naturalist*, 132, 87-106.
- **Mooney**, H.A., P.M. Vitousek, and P.A. Matson, 1987: Exchange of materials between the biosphere and atmosphere. *Science*, **238**, 926-932.
- Moore, J., 1990: Effects of climate change on rangelands. In: World Resources. Oxford University Press, Oxford, UK, pp. 111-116.
- Morello, J., N.E. Crudelli, and M. Saraceno, 1971: La Vegetacion de la Republica Argentina. Los Vinalarer de Formosa (la Colonizodova Leñosa Prosopsis ruscifolia Gris.). INTA, Buenos Aires, Argentina.
- Morison, J.I.L. 1987. Intercellular CO₂ concentration and stomatal response to CO₂. In: Stomatal Function [Zeiger, E., G.D. Farquhar, and I. Cowan (eds.)]. Stanford University Press, Stanford, CA, pp. 229-251.
- **Mosier**, A.R., D. Schimel, D. Valentine, K. Bronson, and W. Parton, 1991: Methane and nitrous oxide fluxes in native, fertilized and cultivated grasslands. *Nature*, **350**, pp. 330-332.
- Murray, D.F., 1980: Balsam poplar in arctic Alaska. Canadian Jounal of Anthropology, 1, 29-32.
- Nadelhoffer, K.J., A.E. Giblin, G.R. Shaver, and J.A. Laundre, 1991: Effects of temperature and substrate quality on element mineralization in 6 arctic soils. *Ecology*, 72(1), 242-253.
- Nakadai, T. Koizumi, Y. Usami, M. Satoh, and T. Oikawa, 1993: Examination of the method for measuring soil respiration in cultivated land: effect of carbon dioxide concentration on soil respiration. *Ecol. Res.*, 8, 65-71.

- Neilson, R.P., 1993: Vegetation redistribution: a possible biosphere source of CO₂ during climatic change. Water, Air, and Soil Pollution, 70, 659-673.
- Neilson, R.P., 1986: High-resolution climatic analysis and southwest biogeography. Science, 232, 27-34.
- Newton, P.C.D., H. Clark, C.G. Bell, E.M. Glasgow, and B.D. Campbell, 1994: Effects of elevated CO₂ and simulated seasonal changes in temperature on the species composition and growth rate of pasture turves. *Annals of Botany*, 73, 53-59.
- Newton, P.D., H. Clark, C.C. Bell, E.M. Glasgow, K.R. Tate, D.J. Ross, G.W. Yeates, and S. Saggar, 1995: Plant growth and soil processes in temperate grassland communities at elevated CO₂. Global Ecology and Biogeography (in press).
- Nicholson, S.E., 1983: Climate variations in the Sahel and other African regions during the past five centuries. *Journal of Arid Environments*, 1, 3-24.
- Nie, D., H. He, G. Mo, M.B. Kirkham, and E.T. Kanemasu, 1992: Canopy photosynthesis and evapotranspiration of rangeland plants under doubled carbon dioxide in closed-top chambers. *Agriculture Forest Meteorology*, 61, 205-217.
- NRC, 1994: Rangeland Health. National Academy Press, Washington DC, 108 pp.
- **Oberbauer**, S.F. and W.C. Oechel, 1989: Maximum CO₂-assimilation rates of vascular plants on an Alaskan arctic tundra slope. *Holarctic Ecology*, **12(3)**, 312-316.
- Oechel, W.C., S.J. Hastings, G. Vourlitis, and M. Jenkins, 1993: Recent change of arctic tundra ecosystems from a net carbon dioxide sink to a source. *Nature*, 361(6412), 520-523.
- Oechel, W.C. and B.R. Strain, 1985: Native species responses to increased carbon dioxide concentration. In: *Direct Effects of Increasing Carbon Dioxide on Vegetation* [Strain, B.R. and J.D. Cure (eds.)]. DOE/ER-0238, U.S. Department of Energy, NTIS, Springfield, VA, pp. 117-154.
- OIES, 1991: Arid Ecosystem Interactions. Report OIES-6 UCAR, UCAR Office for Interdisciplinary Research, Boulder, CO.
- Ojima, D.S., W.J. Parton, D.S. Schimel, and C.E. Owensby, 1990: Simulated impacts of annual burning on prairie ecosystems. In: Fire in North American Tallgrass Prairies [Collins, S.L. and L.L. Wallace (eds.)]. University of Oklahoma Press, Norman, OK, pp. 99-118.
- Ojima, D.S., D.W. Valentine, A.R. Mosier, W.J. Parton, and D.S. Schimel, 1993a: Effect of land use change and methane oxidation in temperate forest and grassland soils. *Chemosphere*, 2, 675-685.
- Ojima, D.S., W.J. Parton, D.S. Schimel, J.M.O. Scurlock, and T.G.F. Kittel, 1993b: Modelling the effects of climatic and carbon dioxide changes on grassland storage of soil carbon. Water, Air, Soil Pollution, 70(1-4), 643-657
- Ojima, D.S., D.S. Schimel, W.J. Parton, and C.E. Owensby, 1994a: Long- and short-term effects of fire on nitrogen cycling in tallgrass prairie. *Biogeochemistry*, 23, 1-18.
- Ojima, D.S., K.A. Galvin, and B.L. Turner, 1994b: The global impact of landuse change. *Bioscience*, 44(5), 300-304.
- Old, S.M., 1969: Microclimate, fire and plant production in an Illinois prairie. *Ecological Monographs*, 39, 355-384.
- O'Leary, M., 1984: Ecological villains or economic victims: the case of the Rendille of northern Kenya. *Desertification Control Bulletin*, 11, 17-21.
- Ottichilo, W.K., J.H. Kinuthia, P.O. Ratego, and G. Nasubo, 1991: Weathering the Storm—Climate Change and Investment in Kenya. Environmental Policy Series No. 3, Acts Press, Nairobi, Kenya, 91 pp.
- Overdieck, D., 1993. Elevated CO₂ and the mineral content of herbaceous and woody species. Vegetatio, 104/105, 403-411.
- Owensby, C.E., P.I. Coyne, J.M. Ham, L.M. Auen, and A.K. Knapp, 1993: Biomass production in a tallgrass prairie ecosystem exposed to ambient and elevated CO₂. *Ecological Applications*, **3**, 644-653.
- Parton, W.J., J.M.O. Scurlock, D.S. Ojima, D.S. Schimel, D.O. Hall, and SCOPEGRAM Group Members, 1995: Impact of climate change on grassland production and soil carbon worldwide. *Global Change Biology*, 1, 13-22.
- Parton, W.J., J.M.O. Scurlock, D.S. Ojima, T.G. Gilmanov, R.J. Scholes, D.S. Schimel, T. Kirchner, J.C. Menaut, T. Seastedt, E. Garcia Moya, A. Kamnalrut, and J.L. Kinyamario, 1993: Observations and modeling of biomass and soils organic matter dynamics for the grassland biome worldwide. Global Biogeochemical Cycles, 7(4), 785-809.

- Parton, W.J., B. McKeown, V. Kirchner, and D. Ojima, 1992: CENTURY Users' Manual. Natural Resource Ecology Laboratory, Colorado State University, Fort Collins, CO.
- Parton, W.J., D.S. Schimel, C.V. Cole, and D.S. Ojima, 1987: Analysis of factors controlling soils organic matter levels in Great Plains Grasslands. Soil Science Society of America Journal, 51, 1173-1179.
- Parton, W.J., J.W.B. Stewart, and C.V. Cole, 1988: Dynamics of C, N, P, and S in grassland soils: a model. *Biogeochemistry*, 5, 109-131.
- Parton, W.J., D.S. Schimel, D.S. Ojima, and C.V. Cole, 1994: A general model for soil organic matter dynamics: sensitivity to litter chemistry, texture and management. In: *Quantitative Modeling of Soil Forming Processes* [Bryant, R.B. and R.W. Arnold (eds.)]. SSSA Spec. Publ. 39. ASA, CSSA and SSA, Madison, WI, pp. 137-167.
- Payne, N.F. and F.C. Bryant, 1994: Techniques for Wildlife Habitat Management of Uplands. McGraw-Hill, New York, 840 pp.
- Polley, H.W., H.R. Johnson, B.D. Marino, and H.S. Mayeux, 1993a: Increase in C₃ plant water-use efficiency and biomass over glacial to present CO₂ concentrations. *Nature*, 361, 61-64.
- Polley, H.W., H.B. Johnson, and H.S. Mayeux, 1994: Increasing CO₂: comparative responses of the C₄ grass Schizachyrium and grassland invader Prosopis. *Ecology* (in press).
- Poppi, D.P., D.J. Minson, and J.H. Ternouth, 1981: Studies of cattle and sheepeating leaf and stem fractions of grasses. I. The voluntary intake, digestibility and retention time in reticulo-rumen. Australian Journal of Agricultural Research, 32, 99-108.
- Prather, M., R. Derwent, D. Ehhalt, P. Fraser, E. Sanhueza, and X. Zhou, 1995: Other trace gases and atmospheric chemistry. In: Climate Change 1994: Radiative Forcing of Climate Change and an Evaluation of the IPCC IS92 Emission Scenarios [Houghton, J.T., L.G. Meira Filho, J. Bruce, H. Lee, B.A. Callander, E. Haites, N. Harris, and K. Maskell (eds.)]. Cambridge University Press, Cambridge, UK, pp. 75-126.
- Prentice, K.C., W. Cramer, S.P. Harrison, R. Leemans, R.A. Monserud, and A.M. Solomon, 1992: A global biome model based on plant physiology and dominance, soil properties, and climate. *Journal of Biogeography*, 19, 117-134.
- Prentice, K.C. and I.Y. Fung, 1990: The sensitivity of terrestrial carbon storage to climate change. *Nature*, 346, 48-51.
- Raison, R.J., 1979: Modification of the soil environment by vegetation fires with particular reference to nitrogen transformations: a review. *Plant and Soil*, 51, 73-108.
- Reibsame, W.E., 1990: Anthropogenic climate change and a new paradigm of natural resource planning. *Professional Geographer*, **42(1)**, 1-12.
- Risser, P.G. and W.J. Parton, 1982: Ecological analysis of tallgrass prairie: nitrogen cycle. *Ecology*, 63, 1342-1352.
- Risser, P.G., E.C. Birney, H.D. Blocker, S.W. May, W.J. Parton, and J.A. Weins, 1981: The True Prairie Ecosystem. Hutchinson Ross, Stroudsburg, PA, 557 pp.
- Riveros, F., 1993: Grasslands for our world. In: Proceedings of the XVII International Grassland Congress. pp. 15-20.
- Rogers, H.H., G.B. Runion, and S.V. Drupa, 1994: Plant responses to atmospheric CO₂ enrichment with emphasis on roots and the rhizosphere. Environmental Pollution, 83, 155-189.
- Rosenzweig, M.L., 1968: Net primary productivity of terrestrial communities: prediction from climatological data. *American Naturalist*, **102**, 67-74.
- Rozema, J., H. Lambers, S.C. van de Geijn, and M.L. Cambridge, 1993: CO₂ and Biosphere. Kluwer Academic Publishers, Boston, MA, 484 pp.
- Rutherford, M.C., 1980: Annual plant production-precipitation relations in arid and semiarid regions. South African Journal of Science, 76, 53-56.
- Running, S.W. and E.R. Hunt, Jr., 1993: Generalization of a forest ecosystem process model for other biomes, BIOME-BGC, and an application for global-scale models. In: Scaling Processes Between Leaf and Landscape Levels [Ehleringer, J.R. and C. Field (eds.)]. Academic Press, Orlando, FL, pp. 141-158.
- Rychnovska, M., 1992: Temperate seminatural grasslands of Eurasia. In: Natural Grassland. Elsevier, Amsterdam and New York, pp. 125-163.
- Sala, O.E., W.K. Laurenroth, and W.J. Parton, 1992: Long-term soil water dynamics in the short-grass steppe. *Ecology*, 73, 1175-1181.
- Sala, O.E., R.A. Golluscio, W.K. Lauenroth, and A. Soriano, 1989: Resource partitioning between shrubs and grasses in the Patagonian steppe. *Oecologia*, 81, 501-505.

- Sala, O.E., W.J. Parton, L.A. Joyce, and W.K. Lauenroth, 1988: Primary production of the central grasslands region of the United States. *Ecology*, 69, 40-45.
- Sampson, R.N., M. Apps, S. Brown, et al., 1993: Workshop summary statement: terrestrial biospheric carbon fluxes—quantification of sinks and sources of CO₂. Water, Air and Soil Pollution, 70, 3-15.
- Sandford, S., 1983: Management of Pastoral Development in the Third World. John Wiley, New York, NY, 316 pp.
- Sarmiento, G., 1983: The savannas of tropical America. In: *Tropical Savannas* [Bourliere, F. (ed.)]. Elsevier, Amsterdam, Netherlands, pp. 245-288.
- Sarmiento, G., 1984: The Ecology of Neotropical Savannas. Harvard University Press, Cambridge, MA, 235 pp.
- Sarmiento, G. and M. Monasterio, 1983: Life forms and phenology. In: Ecosystems of the World 13. Tropical Savannas [Bourliere, F. (ed.)]. Elsevier, Amsterdam, Netherlands, pp. 79-108.
- Sarmiento, G., G. Goldstein, and F. Meinzer, 1985: Adaptative strategies of woody species in neotropical savannas. *Biological Reviews*, 60, 315-355.
- Schimel, D.S., B.H. Braswell, Jr., E.A. Holland, R. McKeown, D.S. Ojima, T.H. Painter, W.J. Parton, and A.R. Townsend, 1994: Climatic, edaphic, and biotic controls over carbon and turnover of carbon in soils. *Global Biogeochem. Cycles*, 8, 279-293.
- Schimel, D.S., 1988. Calculation of microbial growth efficiency from nitrogen-15 immobilization. *Biogeochemistry*, 6(3), 239-243.
- Schimel, D.S., T.G.F. Kittel, and W.J. Parton, 1991: Terrestrial biogeochemical cycles—global interactions with the atmosphere and hydrology. Tellus Series A—Dynamic Meteorology and Oceanography, 43(4), 188-203.
- Schimel, D.S., W.J. Parton, T.G.F. Kittel, D.S. Ojima, and C.V. Cole, 1990: Grassland biogeochemistry: links to atmospheric processes. *Climatic Change*, 17, 13-25.
- Schlesinger, W.H., J.F. Reynolds, G.L. Cunningham, L.F. Huenneke, W.M. Jarrell, R.A. Virginia, and W.G. Whitford, 1990: Biological feedbacks in global desertification. *Science*, 247, 1043-1048.
- Schofield, C.J. and E.H. Bucher, 1986: Industrial contributions to desertification in South America. *Trends in Ecology and Evolution*, 1, 78-80.
- Scholes, R.J., 1993: Nutrient cycling in semi-arid grasslands and savannas: its influence on pattern, productivity and stability. In: *Proceedings of the* XIV International Grassland Congress. 2304 pp.
- Scholes, R.J. and B.H. Walker, 1993: An African Savanna—Synthesis of the Nylsvley Study. Cambridge Studies in Applied Ecology and Resource Management, Cambridge University Press, Cambridge, UK, 306 pp.
- Seastedt, T.R. and A.K. Knapp, 1993: Consequences of nonequilibrium resource availability across multiple time scales: the transient maxima hypothesis. *American Naturalist*, 141, 621-633.
- Seastedt, T.R., J.M. Briggs, and D.J. Gibson, 1991: Controls of nitrogen limitation in tallgrass prairie. *Oecologia* (Berlin), 87, 72-79.
- Silva, J.F., J. Raventos, H. Caswell, and M.A. Trevisan, 1991: Population responses to fire in a tropical savanna grass, Andropogon semiberbis: a matrix model approach. *Journal of Ecology*, 79, 345-356.
- Sims, P.L., 1988: Grasslands. In: North American Terrestrial Vegetation [Barbour, M.G. and W.D. Billings (eds.)]. Cambridge University Press, New York, NY, 434 pp.
- Sinclair, A.R.E. and M. Norton-Griffiths (eds.), 1979: Serengeti: Dynamics of an Ecosystem. University of Chicago Press, Chicago, IL, 389 pp.
- Skarpe, C., 1990: Shrub layer dynamics under different herbivore densities in an arid savanna, Botswana. *Journal of Applied Ecology*, 27, 873-885.
- Smith, D.D., B.R. Strain and T.D. Sharkey, 1987. Effects of CO₂ enrichment on four Great Basin grasses. Functional Ecology, 1, 139-143.
- Solbrig, O., G. Goldstein, E. Medina, G. Sarmiento, and J.F. Silva, 1992: Responses of tropical savannas to stress and disturbance: a research approach. In: Ecosystem Rehabilitation. Vol. 2, Ecosystem Analysis and Synthesis [Wali, M.K. (ed.)]. SPB Academica Publishing, The Hague, Netherlands, pp. 63-73.
- Solomon, A.M., I.C. Prentice, R. Leemans, and W.P. Cramer, 1993: The interaction of climate and land use in future terrestrial carbon storage and release. Water, Air, and Soil Pollution, 70, 595-614.
- Solomon, A.M. and H.H. Shugart (eds.), 1993: Vegetation Dynamics and Global Change. Chapman and Hall, New York, NY, 337 pp.
- Soriano, A., 1992: Rio de la Plata grasslands. In: Natural Grasslands: Introduction and Western Hemisphere [Coupland, R.T. (ed.)]. Elsevier, Amsterdam, Netherlands, pp. 367-408.

- Sperling, L., 1987: Wage employment among Samburu pastoralists of north central Kenya. Research in Economic Anthropology, 9, 167-190.
- Spicer, R.A. and J.L. Chapman, 1990: Climate change and the evolution of high-latitude terrestrial vegetation and floras. *Trends in Ecology and Evolution*, 5(9), 279-284.
- Stafford Smith, D.M., 1993: A Regional Framework for Managing the Variability of Production in the Rangelands of Australia. Defining Stocking Rates for Viable and Sustainable Production in the Face of Market and Climatic Variability. CSIRO/RIRDC Project CSW-28A.
- Stafford Smith, D.M., 1994: Sustainable Production Systems and Natural Resource Management in the Rangelands. ABARE Outlook Conference.
- Stafford Smith, D.M. and G. Pickup, 1993: Out of Africa, looking in: understanding vegetation change. In: *Range Ecology at Disequilibrium* [Behnke, R., I. Scoones, and C. Keerven (eds.)]. Overseas Development Institute, London, UK, pp. 196-244.
- Stafford Smith, D.M. and S.R. Morton, 1990: A framework for the ecology of arid Australia. *Journal of Arid Environments*, 18, 255-278.
- Stafford Smith, M., B. Campbell, W. Steffen, S. Archer, and D. Ojima, 1995:
 GCTE Task 3.1.3: Global Change Impacts on Pastures and Rangelands.
 Implementation Plan. Global Change and Terrestrial Ecosystems Report
 No. 3, GCTE Core Project Office, Canberra, Australia.
- Stephenson, N.L., 1990: Climatic control of vegetation distribution: the role of the water balance. American Naturalist, 135, 649-670.
- Strain, B.R. and J.D. Cure (eds.), 1985: Direct Effects of Increasing Carbon Dioxide on Vegetation. DOE/ER-0238, Carbon Dioxide Research Division, U.S. Department of Energy, Washington DC, 286 pp.
- Suriano, J.M., L.H. Perpozzi, and D.E. Martinez, 1992: El cambio global: tendencias climáticas en la Argentina y el mundo. Ciencia Hoy, 3, 32-39.
- **Tate**, K.R., 1992: Assessment, based on a climosequence of soils in tussock grasslands, of soil carbon storage and release in response to global warming. *Journal of Soil Science*, **43**, 697-707.
- Tate, K.R., D.J. Giltrap, A. Parshotam, A.E. Hewitt, and D.J. Ross, 1995: Impacts of climate change on soils and land systems in New Zealand. In: *Greenhouse '94*. CSIRO Australia (in press).
- **Terri**, J.A. and L.G. Stowe, 1976: Climatic patterns and the distribution of C₄ grasses in North America. *Oecologia* (Berlin), 23, 1-12.
- **Thornley**, J.H.M., D. Fowler, and M.G.R. Cannell, 1991: Terrestrial carbon storage resulting from CO₂ and nitrogen fertilization in temperate grasslands. *Plant, Cell and Environment*, **14**, 1007-1011.
- **Thornley**, J.H.M. and E.L.J. Verberne, 1989: A model of nitrogen flows in grassland. *Plant, Cell and Environment*, **12**, 863-886.
- Tieszen, L.L., M.M. Senyimba, S.K. Imbamba, and J.H. Troughton, 1979: The distribution of C₃ and C₄ grasses and carbon isotope discrimination along an altitudinal and moisture gradient in Kenya. *Oecologia* (Berlin), 37, 337-350.
- **Tissue**, D.L. and W.C. Oechel, 1987: Physiological response to Eriphorum vaginatium to field elevated CO₂ and temperature in the Alaskan tussock tundra. *Ecology*, **68**, 401-410.
- **Titlyanova**, A.A., R.I. Zlotin, and N.R. French, 1990: Changes in structure and function of temperate grasslands under the influence of man. In: *Managed Grasslands (Regional Studies)*. Elsevier, Amsterdam and New York, pp. 301-334.
- Torn, M.S. and J.S. Fried, 1992: Predicting the impacts of global warming on wildland fire. *Climatic Change*, 21, 257-274.
- **Towne**, G. and C.E. Owensby, 1984: Long-term effects of annual burning at different dates in ungrazed Kansas tallgrass prairie. *Journal of Range Management*, **37**, 392-397.
- **Townsend**, A.R., P.M. Vitousek, and E.A. Holland, 1992: Tropical soils could dominate the short-term carbon cycle feedbacks to increased global temperatures. *Climate Change*, **22**, 293-303.
- **Turner**, C.L., T.R. Seastedt, and M.I. Dyer, 1993: Maximization of above ground grassland production: the role of defoliation frequency, intensity and history. *Ecological Applications*, **3**, 175-186.
- Valentine, D.W., E.A. Holland, and D.S. Schimel, 1994: Ecosystem and physiological controls over methane production in northern wetlands. *JGR-Atmospheres*, 99, 1563-1571.
- Van Vegten, J.A., 1983: Thornbush invasion in a savanna ecosystem in eastern Botswana. Vegetatio, 56, 3-7.

- VEMAP Participants, 1995: Vegetation/Ecosystem Modeling and Analysis Project (VEMAP): Assessing biogeography and biogeochemistry models in a regional study of terrestrial ecosystem responses to climate change and CO₂ doubling. Global Biogeochemical Cycles (in press).
- Walker, B.H., 1993: Rangeland ecology: understanding and managing change. Ambio, 22(23), 80-87.
- Walter, H., 1968: Die vegetation der Erde in óko-physiologischer Bertrachtung. Gustav Fischer Verlag, Stuttgart, Germany, 935 pp.
- Walter, H., 1973: Vegetation of the Earth in Relation to Climate and the Eco-Physiological Conditions. Springer-Verlag, New York, NY, 237 pp.
- Walter, H., 1979: Vegetation of the Earth and Ecological Systems of the Geobiosphere. Heidelberg Science Library, Springer-Verlag, New York, NY, 2nd ed., 274 pp.
- Ward, G.M., K.G. Doxtader, W.C. Miller, and D.E. Johnson, 1993: Effects of intensification of agricultura practices on emission of greenhouse gases. *Chemosphere*, 26, 87-94.
- Weaver, J.E. and F.W. Albertson, 1944: Nature and degree of recovery of grassland from the great drought of 1933 to 1940. *Ecological Monographs*, 14(4), 393-497.
- Webb, W.L., W.K. Lauenroth, S.T. Szarek, and R.S. Kinerson, 1983: Primary production and abiotic controls in forests, grasslands, and desert. *Ecology*, 64, 134-151.
- Webb, W., S. Szarek, W.K. Laurenroth, and R. Kinerson, 1978: Primary production and water use in native forest, grassland and desert ecosystems. *Ecology*, 59, 1239-1247.
- Wedin, D.A. and D. Tilman, 1990: Species effects on nitrogen cycling: a test with perennial grasses. *Oecologia*, 84, 433-441.
- Westoby, M., B. Walker, and I. Noy-Meir, 1989: Opportunistic management for rangelands not at equilibrium. *Journal of Range Management*, 42, 26-274.
- Whetton, P., 1993: New climate change scenarios. Climate Change Newsletter, 5(2), 7-8.
- Whisenant, S.G., 1990: Changing fire frequencies on Idaho's Snake River Plains: ecological and management implications. In: Proceedings Cheatgrass Invasion, Shrub Dieoff, and Other Aspects of Shrub Biology, and Management. USDA Forest Service Inter-mountain Research Station, Gen. Tech. Report INT-276, pp. 4-10.

- White, R.G. and J. Trudell, 1980: Habitat preference and forage consumption by reindeer and caribou near Atkasook, Alaska. Arctic and Alpine Research, 12, 511-529.
- Whiting, G.J. and J.P. Chanton, 1993: Primary production control of methane emissions from wetlands. *Nature*, 36, pp. 794-799.
- Williams, J.B. and G.O. Batzli, 1982: Pollination and dispersion of five species of lousewort (Pedicularis) near Atkasook, Alaska. Arctic and Alpine Research, 14, 59-74.
- Wong, S.C., I.R. Cowan, and G.D. Farquhar, 1979: Stomatal conductance correlates with photosynthetic capacity. *Nature*, 282, 424-426.
- Wookey, P.A., A.N. Parsons, J.M. Welker, J.A. Potter, T.V. Callaghan, J.A. Lee, and M.C. Press, 1993: Comparative responses of phenology and reproductive development to simulated environmental change in subarctic and high arctic plants. *Oikos*, 67, 490-502.
- WRI, 1992: World Resources, 1992-1993: A Guide to the Global Environment, Toward Sustainable Development. Oxford University Press, New York and Oxford, 400 pp.
- Yavitt, J.B., J.A. Simmona, T.J. Fahey, 1993: Methane fluxes in a northern hardwood forest ecosystem in relation to acid precipitation. *Chemosphere*, 26, 721-730.
- Yienger, J.J., and H. Levy II, 1995: Global inventory of soil biogenic NO_x emissions. *JGR-Atmospheres* (in press).
- Zak, D.R., K.S. Pregitzer, P.S. Curtis, J.A. Teeri, R. Fogel, and D.L. Randlett, 1993. Elevated atmospheric CO₂ and feedback between carbon and nitrogen cycles. *Plant and Soil*, **151**, 105-117.
- Zimov, S.A., I.P. Semiletov, and Y.V. Voropaev, 1993a: Wintertime CO₂ emission from soils of northeastern Siberia. Arctic, 46(3), 197-204.
- Zimov, S.A., G.M. Zimova, S.P. Daviodov, and A.I. Daviodova, 1993b: Winter biotic activity and production of CO₂ in Siberian soils—a factor in the greenhouse effect. *Journal of Geophysical Research—Atmospheres*, 98(3), 5017-5023.